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# Safaa Ahmed Hamdan Alghasyah Aldhanhani

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United Arab Emirates University

College of Food and Agriculture

COMPARATIVE STUDY OF NUTRIENT UPTAKE BETWEEN  
*SORGHUM X DRUMMONDII* AND *CYPERUS CONGLOMERATUS*, A  
DESERT SEDGE NATIVE TO THE UAE

Safaa Ahmed Hamdan Alghasyah Aldhanhani

This dissertation is submitted in partial fulfilment of the requirements for the degree  
of Doctor of Philosophy

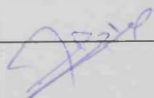
Under the Supervision of Dr. Elke Neumann

September 2016

## Declaration of Original Work

I, Safaa Ahmed Hamdan Alghasyah Aldhanhani, the undersigned, a graduate student at the United Arab Emirates University (UAEU), and the author of this dissertation entitled "*Comparative study of nutrient uptake between sorghum x drummondii and cyperus conglomeratus, a desert sedge native to the UAE*", hereby, solemnly declare that this dissertation is my own original research work that has been done and prepared by me under the supervision of Dr. Elke Neumann, in the College of Food and Agriculture at UAEU. This work has not previously been presented or published, or formed the basis for the award of any academic degree, diploma or a similar title at this or any other university. Any materials borrowed from other sources (whether published or unpublished) and relied upon or included in my dissertation have been properly cited and acknowledged in accordance with appropriate academic conventions. I further declare that there is no potential conflict of interest with respect to the research, data collection, authorship, presentation and/or publication of this dissertation.

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Date: 4/10/2016

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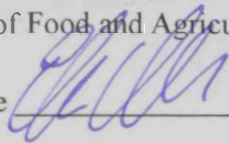
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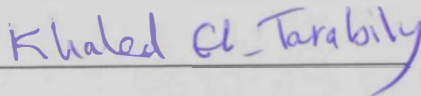
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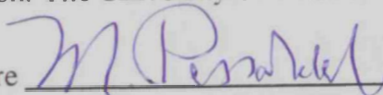
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## Abstract

Sudan grass (*Sorghum x drummondii*) is commonly grown for the production of animal fodder in the UAE. *Cyperus conglomeratus* (locally termed 'Thenda') is a sedge native to the UAE, and one of the very few plants that colonize soils of shifting desert dunes. The native plant is grazed by camels, and may thus have a potential for animal feed production. While Sudan grass is a mycotrophic plant that normally lives in symbiosis with arbuscular mycorrhizal fungi for facilitation of nutrient uptake, *C. conglomeratus* is a non-host to these root symbionts. In the desert sedges rhizosheaths comprising of dense coats of root hairs and entangled soil particles seem to constitute an alternative strategy to support nutrient acquisition. One objective of this study was to compare nutrient uptake from soils of the UAE between Sudan grass and *C. conglomeratus*. Another aim was to investigate how removal of biomass and presence of soil salinity, alone or in combination, would affect the development and functioning of arbuscular mycorrhizal symbioses in Sudan grass grown on a sandy soil of the UAE. In a field experiment, Sudan grass and *C. conglomeratus* were either sole cropped or intercropped under two different irrigation regimes. After 7 months of cultivation, *C. conglomeratus* plants had produced more biomass, and had taken up larger quantities of nutritional elements compared with Sudan grass, even though these plants had received smaller amounts of fertilizers. Neither Sudan grass nor *C. conglomeratus* growth differed depending on whether plants were sole- or intercropped. This may suggest that the two plant species under investigation utilized different pools of nutritional elements, and thus competed only little for nutrient uptake. There was no effect of the water supply level on the growth of intercropped or sole cropped plants, possibly because the water supply level was in a sufficient range even for the plots of the lower water supply treatment. Results of a pot experiment where Sudan grass and *C. conglomeratus* were grown with approximately half of their root systems sharing the same soil volume, confirm the hypothesis that the two plant species under investigation do not compete for the same pools of phosphate (P). However, *C. conglomeratus* growth and nutrient uptake was negatively affected by the presence of a mycorrhiza fungal colonized root system. This confirms the results of the previous pot experiments that reported a direct negative effect of mycorrhizal root systems on the growth of the neighboring non-hosts. The majority of agricultural soils in the UAE

are prone to salinization. It was hypothesized that on saline soil, arbuscular mycorrhiza fungal root colonization and plant mechanisms of adaptation to a saline environment would compete for photoassimilates. Such competitive effects would aggravate upon removal of photosynthetic tissues, and lead to a decline in the development and functioning of mycorrhizae. The null or alternative hypothesis, results indicated that neither salinity nor severe leaf pruning, alone or in combination, had an effect on the relative contribution of arbuscular mycorrhiza fungal symbiosis to plant growth and nutrient uptake. There was also no effect of leaf removal or salinity on the extent by which roots were colonized by endomycorrhizal fungi at the time of harvest. These results suggest that contributions of arbuscular mycorrhiza fungal root colonization to plant performance are relatively robust, and may persist under a wide range of environmental conditions and agricultural practices. Future studies should further shed light into mechanisms by which *C. conglomeratus* mobilizes nutritional elements. As the plant seems to have a great potential to increase nutrient utilization efficiency in agricultural systems of the UAE, its value for animal feed production should be further assessed. Given the superiority of *C. conglomeratus* over Sudan grass in terms of growth and nutrient uptake, it seems unlikely that introduced mycotrophic grasses have the potential to outcompete native dune sedges when released into UAE plant ecosystems.

**Keywords:** Nutrient acquisition, Rhizosphere, Interspecific competition, Rhizosheaths, Arbuscular mycorrhizal.

## Title and Abstract (in Arabic)

دراسة مقارنة لامتناس العناصر المغذية بين نبات حشيشة السودان ونبات التندا  
(نبات صحراوي محلي في الإمارات العربية المتحدة)

### الملخص

تزرع حشيشة السودان (*Sorghum x drummondii*) لإنتاج العلف الحيواني في دولة الإمارات العربية المتحدة. أما نبات التندا (*Cyperus conglomeratus*) فهو نبات محلي في دولة الإمارات العربية المتحدة، وإحدى النباتات القليلة التي تستعمر الكثبان الرملية الصحراوية، وهي من النباتات المحلية التي تتغذى عليها الإبل، ولذلك قد يكون لهذا النبات إمكانية لإنتاج العلف الحيواني. إن حشيشة السودان تعيش عادة في علاقة تكافلية مع فطر المايكورايزا (arbuscular mycorrhizal) لتسهيل امتصاص العناصر الغذائية، بينما لا تتوفر هذه العلاقة التكافلية في نبات التندا. تقوم النباتات الصحراوية (sedges) بتشكيل أغشية كثيفة من شعيرات الجذور وجزيرات التربة المتشابكة (rhizosheaths)، لتشكل إستراتيجية بديلة لدعم اكتساب العناصر الغذائية. إن أحد أهداف هذه الدراسة كان المقارنة بين حشيشة السودان ونبات تندا من حيث امتصاص العناصر المغذية من ترب دولة الإمارات العربية المتحدة. الهدف الآخر لهذه الدراسة كان البحث في كيفية لتربة، منفصلين أو مجتمعين معا، في نمو ووظيفة المايكورايزا في حشيشة السودان الذي ينمو في التربة الرملية لدولة الإمارات العربية المتحدة. في التجربة الحقلية، تمت زراعة حشيشة السودان ونبات تندا بشكل وحيد أو متداخلان، تحت نظامي ري مختلفين. بعد سبعة شهور من الزراعة، أنتجت نباتات التندا كتلة عضوية أكثر وامتصت كميات أكبر من العناصر المغذية مقارنة بحشيشة السودان، بالرغم من أن هذه النباتات أضيفت إليها كميات أقل من الأسمدة. إن نمو حشيشة السودان وكذلك نبات التندا لم يختلف سواء كان النبات زرع وحيدا أو متداخل مع النبات الآخر، هذا يعود الى أن حشيشة السودان ونبات التندا ربما استعملا تجمعات مختلفة من العناصر المغذية، وكان هناك تنافس قليل لامتناس لنباتات سواء كانت مزروعة وحيدة أو متداخلة، من المحتمل أن السبب في ذلك هو أن مستوى الري كان في مدى كافي حتى في المعاملات ذات مستويات ري منخفض. إن نتائج تجربة الأصص، حيث اشتركت نصف جذور بة، تؤكد فرضية أن حشيشة السودان ونبات التندا لا يتنافسان على نفس تجمعات الفوسفات. كما بينت الدراسة نمو نبات التندا وامتصاصه

للعناصر المغذية تأثر سلبيًا بوجود المايكورايزا، وهذا يؤكد نتائج تجارب الأصص السابقة التي ذكرت التأثير السلبي المباشر للمايكورايزا في نمو النبات المجاور الذي لا يعيش عليه الفطر. إن غالبية الترب الزراعية في دولة الإمارات العربية المتحدة عرضة للملوحة. ومن المفترض أن المايكورايزا وآليات تكيف النبات في البيئة الملحية تتنافس على بعض المركبات الناتجة من عملية البناء الضوئي، إن مثل هذه التأثيرات التنافسية تزيد من إزالة الأنسجة التي تقوم بعملية البناء الضوئي وتؤدي إلى انخفاض في نمو ووظيفة المايكورايزا. ولكن خلافا لهذه الفرضية، أشارت النتائج بأن الملوحة والتقليم الحاد للأوراق، كل على حده أو مجتمعين لم يؤثر على المساهمة النسبية للمايكورايزا في نمو النبات وامتصاصه للعناصر المغذية، كذلك لا يوجد تأثير لإزالة الأوراق أو الملوحة على امتداد الجذور التي لقحت بالمايكورايزا في وقت الحصاد. تقترح هذه النتائج أن هناك مساهمات كبيرة من قبل المايكورايزا في أداء النبات وقد تستمر تحت مختلف الظروف البيئية والممارسات الزراعية. الدراسات المستقبلية يجب أن تسلط ضوء على الآليات التي ينقل فيها نبات التندا العناصر المغذية. ويبدو أن نبات التندا يمتلك إمكانية عظيمة لزيادة كفاءة استخدام العناصر المغذية في الأنظمة الزراعية لدولة الإمارات العربية المتحدة، كما إن قيمته الغذائية واستخدامه كعلف حيواني يجب أيضا أن تقيم إلى حد أبعد. تفوق نبات التندا على حشيشة السودان من ناحية النمو وامتصاص العناصر المغذية يشير إلى إمكانية أن إدخال النبات المرتبط بالمايكورايزا يؤدي إلى تنافس وإزاحة نباتات الكتبان الرملية المحلية في الأنظمة البيئية في دولة الإمارات العربية المتحدة.

**مفاهيم البحث الرئيسية:** اكتساب العناصر المغذية، التربة المحيطة بالجذور، المنافسة بين الأنواع، الأغشية الكثيفة، المايكورايزا.



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Thanks are placed before my parents for encouraging me to fulfil my dreams. Thank you for providing me with constructive opportunities to explore the many paths life has to offer. I thank you for your love and admire your wisdom and strength.

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## Dedication

*To my beloved family*

## Table of Contents

Title.....	i
Declaration of Original Work .....	ii
Copyright.....	iii
Advisory Committee .....	iv
Approval of the Doctorate Dissertation .....	v
Abstract.....	vii
Title and Abstract (in Arabic) .....	ix
Acknowledgements.....	xi
Dedication. ....	xiii
Table of Contents.....	xiv
List of Tables.....	xvii
List of Figures .....	xix
List of Abbreviations.....	xxi
Foreword.....	1
Chapter 1: Comparison of nutrient uptake between sole- or intercropped <i>Cyperus conglomeratus</i> and Sudan grass in the field.....	10
1.1 Introduction.....	10
1.2 Materials and Methods.....	14
1.2.1 Plant material and seeding preparation .....	14
1.2.2 Set up of the field experiment .....	14
1.2.3 Installation of a root monitoring window.....	16
1.2.4 Maintenance of the experiment in the field.....	17
1.2.5 Harvest and dry weight .....	22
1.2.6 Analysis of the plant material for element concentrations and contents .....	23
1.2.7 Statistical analysis .....	24
1.3 Results.....	26
1.3.1 Rooting density beneath <i>C. conglomeratus</i> and Sudan grass plants .....	26
1.3.2 Formation of aboveground biomass.....	33
1.3.3 Arbuscular mycorrhiza fungal root colonization .....	37
1.3.4 Element analysis.....	39
1.4 Discussion .....	46
1.4.1 Growth and dry matter yield of intercropped versus sole cropped Sudan grass or <i>C. conglomeratus</i> .....	46
1.4.2 Possible reasons for differences in nutrient acquisition between Sudan grass and <i>C. conglomeratus</i> .....	50
1.4.3 The effect of irrigation water supply on plant growth and nutrient uptake .....	55
1.4.4 The effect of water supply, and sole- versus intercropping on the extent of arbuscular mycorrhiza fungal root colonization .....	56

Chapter 2: Comparative study of phosphorus acquisition between Sudan grass and <i>Cyperus conglomeratus</i> .....	58
2.1 Introduction.....	58
2.2 Materials and Methods.....	61
2.2.1 Plant material and seedling preparation .....	61
2.2.2 Planting pot and growth substrate preparation .....	62
2.2.3 Maintenance of experiment in the greenhouse.....	64
2.2.4 Harvest and dry weight .....	65
2.2.5 Mycorrhiza root colonization .....	66
2.2.6 Analysis of the plant material for element concentrations and contents .....	66
2.2.7 Statistical analysis .....	67
2.3 Results.....	68
2.3.1 Plant dry weight at the time of the terminal harvest .....	68
2.3.2 Arbuscular mycorrhiza fungal root colonization .....	76
2.3.3 Element analysis.....	77
2.4 Discussion .....	86
2.4.1 Effect of mycorrhiza inoculation on P uptake and growth of Sudan grass and <i>C. conglomeratus</i> grown with roots sharing the same soil volume.....	86
2.4.2 Supply of plants with nutritional elements other than P .....	95
Chapter 3: The effect of clipping on the contribution of arbuscular mycorrhizal fungi to salinity tolerance in the groundcover Sudan grass ( <i>Sorghum x drummondii</i> ).....	99
3.1 Introduction.....	99
3.2 Materials and Methods.....	102
3.2.1 Plant material and seeding preparation .....	102
3.2.2 Growth substrate preparation and filling of the experimental pots .....	104
3.2.3 Establishment of salinity treatments .....	104
3.2.4 Maintenance of the experiment in the greenhouse.....	105
3.2.5 Defoliation of the plants.....	106
3.2.6 The growth measurements of plants.....	106
3.2.7 Estimation of the endomycorrhiza colonized root length mycorrhiza root colonization.....	107
3.2.8 Harvest and dry weight .....	107
3.2.9 Analysis of the plant material for element concentrations and contents .....	108
3.2.10 Statistical analysis .....	108
3.3 Results.....	109
3.3.1 Shoot growth between 71 and 78 days after planting .....	109
3.3.2 Plant dry weight produced throughout the growth period.....	111
3.3.3 Arbuscular mycorrhiza fungal root colonization .....	116
3.3.4 Elements analysis .....	118

3.4 Discussion ..... 133

3.4.1 Effect of soil salinity on the relative contribution of the arbuscular mycorrhiza f ..... s s ..... o ..... 133

3.4.2 Effect of shoot clipping on the relative contribution of the arbuscular mycorrhiza fungal symbiosis to plant growth and nutrient uptake 141

Conclusions..... 145

References..... 148

## List of Tables

Table 1: The weight of rhizosheath in percentage of the total root measured 83 DAP and 224 days after planting (DAP). .....	32
Table 2: Element concentrations in shoot material obtained from Sudan grass and <i>C. conglomeratus</i> plants at the time of the final harvest. ....	40
Table 3: Results of the Two Way ANOVA performed on data obtained for average element concentrations in the shoots of plants of the SC plots under (+) Water or (-) Water supply. ....	41
Table 4: Results of the Two Way ANOVA performed on data obtained for average element concentrations in the shoots of plants of the SS, CC or SC plots under (+) Water supply. ....	42
Table 5: Element content in shoot biomass obtained from Sudan grass and <i>C. conglomeratus</i> plants at the time of the final harvest. ....	43
Table 6: Results of the Two Way ANOVA performed on data obtained for total element content in the shoots of plants of the SC plots under (+) Water or (-) Water supply. ....	44
Table 7: Results of the Two Way ANOVA performed on data obtained for total element content in the shoots of plants of the SS, CC or SC plots under (+) Water supply. ....	45
Table 8: Element concentrations in shoot material obtained from Sudan grass and <i>C. conglomeratus</i> plants in mg per g DW for macronutrients, and in µg per g DW for micronutrients. ....	79
Table 9: Results of the Two Way ANOVA performed on data obtained for element concentrations in the shoots of Sudan grass and <i>C. conglomeratus</i> plants..	81
Table 10: Element content of shoots obtained from Sudan grass and <i>C. conglomeratus</i> plants in mg per plant for macronutrients, and in µg per plant for micronutrients. ....	83
Table 11: Results of the Two Way ANOVA performed on data obtained for element content in the shoots of Sudan grass plants. ....	84
Table 12: Results of the Two Way ANOVA performed on data obtained for element content in the shoots of <i>C. conglomeratus</i> plants. ....	85
Table 13: Element concentrations in shoot material obtained from Sudan grass plants.....	120
Table 14: Results of the Three Way ANOVA performed on data obtained for element concentrations in the shoots of Sudan grass plants.....	122
Table 15: Element content in shoot material obtained from Sudan grass plants in mg per plant. ....	126
Table 16: Results of the Three Way ANOVA performed on data obtained for element content in the shoots of Sudan grass plants. ....	127
Table 17: Element concentrations in root material obtained from Sudan grass plants. ....	129

Table 18: Results of the Three Way ANOVA performed on data obtained for element concentrations in the root of Sudan grass plants. .... 130

Table 19: Element content in root material obtained from Sudan grass plants in mg per plant. .... 131

Table 20: Results of the Three Way ANOVA performed on data obtained for element content in the root of Sudan grass plants. .... 132

## List of Figures

Figure 1: The distribution of the plants and drippers in one intercropped plot of the field experiment.....	16
Figure 2: A root window made out of an acrylic glass Plate installed in the plot planted with <i>C.conglomeratus</i> .....	17
Figure 3: The experiment site in the field at Al Foah Experimental Farm .....	18
Figure 4: Field experiment shortly before the final harvest.....	20
Figure 5: Soil sample with roots by Cork borer (20 cm depth and 2.5 cm diameter) 21	
Figure 6: At the final harvest, plot was divided into four sections (RW, N, M, F) ...	22
Figure 7: Rooting densities measured 83 DAP (in mg root dry weight per cm <sup>3</sup> soil). .....	27
Figure 8: Rooting densities measured 224 DAP (in mg root dry weight per cm <sup>3</sup> soil). .....	29
Figure 9: White roots with dense coats of root hairs were observed beneath <i>C. conglomeratus</i> plants through the root windows.....	30
Figure 10: Typical brownish <i>C. conglomeratus</i> roots.....	31
Figure 11: Total aboveground dry weight formed throughout the whole growth period in kg per plot. ....	34
Figure 12: Total aboveground dry weight formed throughout the whole growth period in g per plant. ....	36
Figure 13: Plants in the field shortly before the final harvest.....	37
Figure 14: The arbuscular mycorrhiza fungal colonized root length in percent of the total root length. ....	39
Figure 15: <i>Cyperus conglomeratus</i> was propagated by rhizome cuttings .....	61
Figure 16: Sudan grass was transplanted as split root to triple planting pots .....	63
Figure 17: The three compartment split root pots in the greenhouse at 2 days after planting. The plastic bags were removed from <i>C. conglomeratus</i> 7 days after transplanting and from Sudan grass 14 days after transplanting ...	65
Figure 18: Shoot dry weight produced by the plants until the final harvest in g per plant.....	70
Figure 19: Dry weight of roots obtained from outer compartment in g per plant.....	72
Figure 20: Root dry weight produced by the plants until the final harvest in g per pot in the shared pots.....	73
Figure 21: Distribution of the total root DW obtained for each triple pot over the inner and outer compartment in %. ....	74
Figure 22: soil attached to the roots in g per g root dry weight in the outer pots. ....	75
Figure 23: Soil attached to the roots in g per g root dry weight in the shared pots. ..	75
Figure 24: The endomycorrhiza colonized root length in percent of the total root length.....	77
Figure 25: The experiment pots in the greenhouse .....	106



Figure 26: Shoot length increment between 71 and 78 days after planting in cm per plant.....	109
Figure 27: Number of tillers increment per plant between 71 and 78 days after planting.....	110
Figure 28: Leaf Number (length >3cm) increment per plant between 71 and 78 days after planting. ....	111
Figure 29: Total dry weight produced by the plants throughout the experimental period in g per plant. ....	112
Figure 30: Contribution of different plant fractions to the total plant dry weight in g per plant.....	114
Figure 31: Contribution of different plant parts to the total plant dry weight in g per plant. ....	115
Figure 32: Shoot/Root Ratio estimated at the final harvest. ....	116
Figure 33: The arbuscular mycorrhiza fungal colonized root length in percent of the total root length. ....	117
Figure 34: Microscopic images of the fungal colonized roots stained with ink .....	117
Figure 35: K/Na ratio in shoot material obtained from Sudan grass plants. ....	123
Figure 36: Ca/Na ratio in shoot material obtained from Sudan grass plants. ....	124

## List of Abbreviations

C*	<i>Cyperus conglomeratus</i>
Cl	Clipping
DAP*	Day after planting
DW*	Dry weight
Myc*	Mycorrhizal inoculation
N*	Neighboring species
Non-Myc*	No mycorrhizal inoculation
Non-Sal*	No salt in irrigation water
S*	Sudan grass
Sal*	Saline
Sp*	Plant species
W*	Water supply level
(+) Water	8L water
(-) Water	4L water

\*Abbreviation used in figures and tables.

## Foreword

*Cyperus conglomeratus* is native to the UAE, and occurs in desert dune ecosystems, wadis and along roadsides across all parts of the country. The Arabic name is 'thenda'. *Cyperus conglomeratus* is grazed by camels, and thus has a potential to be used in low-input forage production systems. However, so far there are no reports on *C. conglomeratus* performance in agro-ecosystems. From observations on the natural distribution of the plant across different habitats, it was concluded that *C. conglomeratus* prefers soils with a low salinity level, high sand content, and slightly alkaline pH (El-Keblawy et al., 2015). Different from many other plants, *C. conglomeratus* cannot only colonize inter-dune plains and wadis, but also slopes and tops of moving sand dunes (Ksiksi et al., 2007; El-Keblawy et al., 2009). Such desert dune habitats are not only subject to continuous soil erosion and deposition, but are also characterized by a very low plant availability of nutritional elements. The natural habitat of *C. conglomeratus* is further characterized by: extreme heat (topsoil temperatures  $> 70^{\circ}\text{C}$ ) during summer, and extreme drought (annual precipitation  $< 100$  mm), with no access to subsurface water pools. The *C. conglomeratus* roots are described as shallow and surrounded by sandy sheaths that comprise of dense root hairs and entangled soil particles. These so-called 'rhizosheaths' might play a role in plant water and nutrient uptake (El-Keblawy et al., 2015), but the precise mechanism of their functioning has not yet been studied.

The majority of the species within the Cyperaceae tested so far have been found non-hosts to mycorrhizal fungi. Several members of the genus *Cyperus*, however, were described as facultatively mycotrophic (Muthukumar et al., 2004). Preliminary microscopic observations of *C. conglomeratus* roots sampled from plants growing in

the UAE found that these were not colonized by mycorrhizal fungi (Neumann E. personal communication). The grand majority of terrestrial plant species live in symbiosis with mycorrhizal fungi, and such associations between plant roots and soil fungi are found in almost all terrestrial ecosystems (Smith and Read, 2008). Mycorrhizal symbioses are evolutionary among the oldest symbiotic associations in nature, and there is evidence that even the earliest landplants formed mutualistic associations with soil fungi (Humphreys et al., 2010; Corradi and Bonfante, 2012).

Based on morphological characteristics of the symbiosis, seven different categories of mycorrhizal symbiosis are distinguished (Finlay, 2008). The most widespread among cultivated plants is the endomycorrhizal symbiosis, which involves arbuscular mycorrhizal fungi. The endomycorrhizal symbiosis is the most ancient type of mutualistic plant-fungal association.

The extraradical mycelium of the arbuscular mycorrhizal fungi greatly extends the nutrient absorbing surface of the plant roots. Phosphate and other nutritional elements taken up by the hyphae are partially transported to the intraradical mycelium, where they are transferred to the plant cytoplasm (Richardson et al., 2011). An improved water status of mycorrhizal plants compared with nonmycorrhizal controls has also been observed in some experiments. The mechanisms behind this appear to be diverse. Some authors could show that arbuscular mycorrhizal mycelia take up water and transport it to the root (Augé et al., 2007). An improved nutritional status of arbuscular mycorrhizal compared with non arbuscular mycorrhizal plants may also contribute to a better ability of arbuscular mycorrhizal plants to grow in dry soil. The presence of the arbuscular mycorrhizal fungal intra- and extraradical hyphal network

might also improve the hydraulic conductivity of the root and the rhizosphere soil, improved nutrient uptake and hydraulic conductance (Bárcana et al., 2014).

Non-hosts are evolutionary younger than the mycotrophic plants. The evolution of non-hosts involved the loss of genes relevant for the establishment of the symbiosis (Delaux et al., 2014). Less than 20 % of all land plants are non-hosts to mycorrhizal fungi (Brundrett, 2009). Non-hosts are prominent among the Amaranthaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae and Proteaceae. Often non-hosts have evolved alternative strategies to acquire nutrients from sparingly available resources in the soil, such as cluster roots or rhizosheaths. Plant species that do not normally form mycorrhizal associations are often found in habitats that are subject to frequent disturbance (Wang and Qiu, 2006; Lambers et al., 2008). *Cyperus conglomeratus* is known to form rhizosheaths, which appear as several mm thick coats of soil around the roots. These water-stable formations are most likely the result of root exudation, root hair proliferation, and microbial activities (Chaboud, 1983; Watt et al., 1993; Read and Gregory, 1997). The mucilage excreted by plants and microorganisms can apparently contribute to the formation of a coherent soil sheath around the roots of some plant species (Chaboud, 1983; Watt et al., 1993; Read and Gregory, 1997). Rhizosheaths can be beneficial in terms of plant performance and ecosystem functioning. For example, they have been shown to stabilize shifting sand, improve soil structure, retain soil moisture, and encourage plant nutrient uptake (Watt et al., 1994; Wei et al., 2011). The mechanisms by which rhizosheaths facilitate plant nutrient acquisition are still not completely understood. It is possible that they contribute to chemical mobilization of sparingly soluble nutritional elements such as P, e.g. through supporting the maintenance of a reduced pH around the plant root. The large amounts of dense root hairs that contribute to rhizosheath formation may provide

additional surface area for nutrient uptake. It is also assumed that rhizosheaths nurture bacterial populations improve plant nutrient availability.

Many plants that are native to the UAE and thrive in desert ecosystems, belong to the Caryophyllaceae, Chenopodiaceae or Cyperaceae, and may thus follow a non-mycotrophic strategy for nutrient acquisition. It is possible that heat, drought, scarcity of vegetation, and susceptibility of the desert soils for wind and water erosion do not allow mycorrhiza fungal networks to persist and to sustain sufficient infective potential. Thus, plants not relying on fungal partners for nutrient acquisition may be more successful in such habitats compared with mycotrophs.

When disturbance is less frequent, either due to progressing natural succession or human intervention, mycotrophic plants may have a competitive advantage over non-hosts. Al-Yahyaie et al. (2011) found that the abundance, diversity and species richness of arbuscular mycorrhizal fungi was much greater in the rooting zone of adult date palms plantation compared with mycotrophic plants growing in a natural ecosystem in the same area.

Most crops and ornamental plants cultivated in the UAE are mycotrophs that are not native to the Gulf Region. Whether these plants would find appropriate symbiotic partners in desert soils of the UAE, has not yet been studied in much detail. The soils of the UAE are slightly alkaline and often rich in calcium carbonate. Phosphorus and micronutrient deficiencies are commonly observed in cultivated plants, but only rarely in the native vegetation. The ability of non-native mycotrophs and native non-hosts to acquire nutritional elements from agricultural soils of the UAE, and to grow under reduced supply of irrigation water, has never been comparatively analyzed. It is also not known whether arbuscular mycorrhizal plants and native non-

hosts would make use of the same or different sources of water and nutritional elements in the soil. In case both strategies would exploit different nutrient and water pools, inclusion of non-hosts into the cultivation system could lead to a particularly efficient utilization of soil nutrient resources. Utilization of the same pools of nutritional elements and water by both strategies would result in interspecific competition.

In the UAE and other countries of the Gulf Region, increasing depletion and pollution of groundwater resources is a major concern. Governmental plans aim at reducing the water expenditure for irrigation, and support water saving production practices. Recently, the cultivation of Rhodes grass for the production of animal fodder was banned in the UAE, as this was known to consume particularly large amounts of irrigation water. However, animal husbandry has a long tradition in the country, and animal fodder is needed to sustain herds of goats, sheep and camels. Whether native plants such as *C. conglomeratus* could be used alone or in combination with non-native grasses to produce animal fodder under a lower input of irrigation water and fertilizers, has not yet been studied.

Particularly in the Northern Emirates, cultivation of Sudan grass for animal fodder production is very common. Sudan grass is a C4 plant native to the Sudan and Egypt. It is a very common forage plant in subtropical areas, and known to tolerate water and nutrient deficiency, as well as moderate salinity. Sudan grass is a mycotrophic plant, and most successful in established ecosystems and agricultural systems where irrigation water and fertilizer are applied (Subramanian et al., 2006; Habibzadeh et al., 2013).



Plants native to the deserts of the Gulf Region often show remarkable adaptations to heat, drought, salinity and low soil nutrient availability. However, so far these native plants are not used much in agricultural production systems. It could be expected that such plants would require less nutrients and water for growth compared with exotic plant species from more humid or temperate regions. On the other hand, desert plants are often expected to produce only little biomass, and to have a poor growth potential.

Exotic (Non native) plants were introduced to the region deliberately or by accident. There are concerns related to the introduction of exotic plant species, as these may impact the native plant vegetation, and outcompete native plants without providing adequate ecosystem services (e.g. feeding native fauna: Jauni and Ramula , 2015). Invasion of exotic plant species can change the habitat and ecosystem functioning (Levine et al., 2003; Ehrenfeld, 2010; Gaertner et al., 2014).

However, though introduced cultivated plants often show a better performance compared with native plants in agroecosystems, it is not known whether they could indeed establish and outcompete native species when no water or nutrients are provided. Daehler, (2003), Denoth and Myers, (2007), Domènech and Vilà, (2008) and Morales and Traveset, (2009) reported that there are no differences between exotic and native plant species in competitive effect on the native plants, but Dillenburg et al. (1993) and Iponga et al.,(2008) found that the exotic plant species are better than native plants in competition and that may influence on coexisting native species (Jauni and Ramula , 2015).

Not only resource competition, but also allelopathic effects may play a role in the interaction between native and exotic plant species. Allelopathy is a mechanism in



plants that causes depressive effect on the associated flora. This is through chemicals releases from roots that affect neighboring plants (Brewer, 2002; Bais et al., 2003; Callaway and Ridenour, 2004). Inderjit et al. (2008) and Stinson et al. (2006) reported that the exotic species may become successful invaders by using this mechanism. For example, *Prosopis juliflora* is an exotic invasive species in the UAE, which is considered a weed because it has come to dominate many plant communities (El-Keblawy and Abdelfattah, 2014). It invades both, natural and managed habitats and crowds out native vegetation (Tiwari, 1999; El-Keblawy and Al-Rawai, 2005, 2007). El-Keblawy and Abdelfattah, (2014) found that the *P. juliflora* inhibited the seed germination of five native plants in the UAE. *Prosopis juliflora* is using allelopathic mechanisms against native species (Goel and Behl, 1998; Inderjit et al., 2008; Kaur et al., 2012). Another reason that facilitated its rapid invasion into new areas is biological characteristics of *P. juliflora* (Shiferaw et al., 2004). In general, physical factors, competition for scarce resources, allelochemicals release into the environment, shading and relative susceptibility to herbivory are determinants of competitive strength in plant species (Callaway et al., 1991).

Arbuscular mycorrhizal fungi belong to the phylum of the Glomeromycota (Redecker et al., 2000), and form symbioses with roots of members of the Angiosperms, Gymnosperms, Pteridophytes and some Bryophytes plants (Smith and Read, 1997). Particularly on soils with a low nutrient availability, the arbuscular mycorrhizal symbiosis improves plant micronutrient and macronutrient uptake (Barea et al., 2005). A contribution of the arbuscular mycorrhizal symbiosis to plant phosphorus acquisition has been observed most frequently (Berta et al., 1995). Some studies demonstrated that mycorrhizal plants had higher photosynthetic rates and biomass compared with nonmycorrhizal controls (van der Heijden et al., 1998, 2006;

Marulanda et al., 2006; Hu and Rufty, 2007). In exchange for their contribution to plant nutrition, host plants provide the symbiotic fungi with carbon (Koide, 1991; Newsham et al., 1995). Under certain conditions, the arbuscular mycorrhizal symbiosis has also been shown to facilitate plant water uptake (van der Heijden et al., 1998, 2006; Marulanda et al., 2006; Hu and Rufty, 2007), and to improve the soil aggregate stability (Rillig, 2004). Over time, the presence of mycorrhizal plants can improve the soil quality in terms of organic matter content, aggregate stability and water infiltration (Rillig, 2004; Schmid et al., 2008).

Arbuscular mycorrhizal fungi are obligate symbionts (Helgason and Fitter, 2005; Smith and Read, 2008; Pringle et al., 2009). The fungi are named after the hyphal structure ('arbuscules') that they form within the cortical cells of roots (Helgason and Fitter, 2005). Arbuscular mycorrhizal colonization is starting with formation of hyphae which grow from large resting spores or mycorrhizal root fragments or from the neighbor arbuscular mycorrhizal plant (Azcon-Aguilar and Barea, 1997). Once initial root colonization is established, the fungal mycelium further spreads within the root cortex, and around the root. The fungal mycelium can also interconnect mycotrophic plant species via producing extensive underground networks. Mycorrhiza root colonization has been shown to impact the functioning and biodiversity of ecosystems (Smith et al., 1997; Bonfante and Genre, 2010). The intraradical mycelium of these obligate biotrophic soil fungi proliferates in the cortex of the host plant root, whereas the extraradical part spreads in the soil around the root. The latter provides the surface area by which the fungus facilitates host plant uptake of nutritional elements from the soil (Rillig, 2004). Furthermore, the arbuscular mycorrhiza fungal mycelium physically entangles soil particles, and thus contributes to soil aggregation and stability (Rillig et al., 2002; Rillig and Mummey, 2006). The hyphae of some mycorrhiza fungal

species even excrete a hydrophobic, glue-like protein ('Glomalin'), which is very stable in the soil and probably involved in the formation of microaggregates (Wright and Upadhyaya, 1998). The highly branched fungal structures and arbuscules are grown intracellularly without penetrating the host plasmalemma and this is the most important point to characterize the symbiosis (Finlay, 2008). Arbuscules are the symbiotic structures inside plant root cells and it is the place where the nutrient exchanges between the fungus and its host (Parniske, 2008).

## Chapter 1: Comparison of nutrient uptake between sole- or intercropped *Cyperus conglomeratus* and Sudan grass in the field

### 1.1 Introduction

In the UAE, all open field plant cultivation systems require irrigation. Grasses in form of tufts are mainly grown for landscaping purposes, to stabilize sand dunes along roads, and for the production of animal feed. Most grass species cultivated in the country are members of the Poaceae, not native to the desert environments of the Gulf region. Tufts of Rhodes- or Sudan grass cultivated under drip irrigation constitute one of the most common animal fodder production systems in the UAE. Despite a governmental ban on commercial Rhodes grass cultivation, many farmers are still growing fodder grasses for their private use.

The cultivation of native plants for fodder production might help farmers in desert regions to reduce the water expenditure for animal husbandry. However, highly drought and heat tolerant plant species like *C. conglomeratus* have not yet been tested for their yield potential in agricultural production systems. The ability of plant species to thrive under adverse climatic or soil conditions is often associated with lower maximal photosynthetic capacity, and a relatively high portion of photoassimilates allocated to stress adaptation mechanisms. For example, to reduce transpiration, drought tolerant plant genotypes often have a lower photosynthetically active surface area per unit dry weight compared with less tolerant ones (Fischer et al., 2014). Plants like *C. conglomeratus*, which is adapted to soils with an extremely low nutrient and water availability, might allocate photoassimilates rather to belowground water and nutrient acquisition strategies than aboveground biomass production. Thus, perennial plants native to desert ecosystems may show greater survival and better performance

compared with plants from less stress-prone areas particularly when exposed to drought, heat and low soil nutrient availability. Though physiologically active native plant species are found in desert ecosystems even during the hot summer months, their growth rates are low, and only low planting densities are maintained. The feasibility of desert plants for agricultural production would depend on their ability to respond to additional input of water and nutrients with increased growth and maintenance of planting densities common to agricultural systems. It is a frequent observation that when growing conditions are improved, the less stress tolerant plant genotypes outperform the stress tolerant ones (Maestre et al., 2009). One aim of the present experiment was to study the growth of *C. conglomeratus* in an agricultural field that receives moderate levels of fertilizer and irrigation water input. It was hypothesized that with increasing water supply, *C. conglomeratus* would form lower amounts of aboveground biomass compared with Sudan grass grown under the same conditions.

Fodder grasses in the UAE are most frequently grown in sole cropping systems. Intercropping is so far rarely used. Intercropping systems of agricultural crops have often been shown to achieve higher cumulative yields per area of land compared with sole cropping systems. The success of an intercropping system, however, mainly depends on two different plant species exploiting different pools of scarce resources, or exploiting the same pools at different times. In successful intercropping systems, such complementary resource utilization leads to a greater resource utilization efficiency of the overall production system.

*Cyperus conglomeratus* and Sudan grass appear to follow distinct strategies for nutrient and possibly water acquisition. Often non-hosts have evolved strategies such as cluster roots or rhizosheaths. However, Sudan grass have used mycorrhizal.

Intercropping systems are most successful when intercropped plants follow different strategies for resource acquisition, and the two plant species used in the current experiment are expected to exploit different pools of nutritional elements in the soil.

Intercropping is two plant species or more growing simultaneously in the same field (Yan et al., 2014). Intercropping system reduces the use of chemical fertilizers and herbicides (Dhima et al., 2007), the fertilizers are effectively utilized (Javanmard et al., 2009) and yield is increased (Dhima et al., 2007), improves the quality of the forage (Bingol et al., 2007; Lithourgidis et al., 2007). The resources efficiency is increased by intercropping system (Knudsen et al., 2004). Weisany et al. (2016) reported that, under intercropping system, there are competitions for soil resources, which is playing a key role in the yield. However, sole cropping is growing one plant species alone in the same field.

The intercropping system was more beneficial in increasing the yields compared with sole cropping system. The reason for the last sentence is the advantages of intercropping system such as utilization of resources (water, N fertilization and light) (Hamzei and Seyyedi, 2016) as well as the nutrient concentrations like P and K were increased under intercropping compared with the sole cropping (Weisany et al., 2016). However, Liebman and Dyck, (1993) found that the weed biomass were decreased in intercropping compared with the sole cropping. Weisany et al. (2016) reported that the weed competition may be reduced by intercropping and that will increase the plant production and showed that, under sole and intercropping systems the arbuscular mycorrhizal had ability to increase competition.

The second hypothesis was that intercropped plots would achieve higher total biomass compared with the sole cropped plots, and that this effect would be more

pronounced with reduced irrigation water supply. The experiment was done in the field to test performance of the two plants under conditions of the UAE and to represent the cultivation in the farm.



## 1.2 Materials and Methods

### 1.2.1 Plant material and seeding preparation

*Cyperus conglomeratus* rhizome cutting were planted in cell trays on day 13<sup>th</sup>, 17<sup>th</sup>, 19<sup>th</sup> and 20<sup>th</sup> of November-2014 and 1<sup>st</sup> of December-2014. *Cyperus conglomeratus* plants were collected from their natural habitat, along a roadside in Al Foah. On 27<sup>th</sup> of January-2015 and 22<sup>nd</sup> of March-2015, Sudan grass seeds were placed in moist filter paper and covered with black polythene sheet under room temperature for germination, and that germination occurred between day 28<sup>th</sup> of January-2015 and day 29<sup>th</sup> of January-2015 and on day 23<sup>rd</sup> of March-2015. The Sudan grass seedlings were transferred to the cell trays on day 29<sup>th</sup> of January-2015 and 23<sup>rd</sup> of March-2015.

The plants were planted in cell trays filled with sieved (1 mm) topsoil from a sand dune near to where the experiment was conducted. Each cell had a volume of 150 cm<sup>3</sup>. The soil had not been used for agricultural activities, and plants were absent from the dune. Each Sudan grass plant was fertilized with 200 mg N (NH<sub>4</sub>NO<sub>3</sub>), 50 mg P (KH<sub>2</sub>PO<sub>4</sub>), 100 mg K (K<sub>2</sub>SO<sub>4</sub>), 100 mg Mg (MgSO<sub>4</sub>·7H<sub>2</sub>O), 20 mg Fe (Fe EDDHA), 15 mg Mn (MnCl<sub>2</sub>·4H<sub>2</sub>O) per kg dry soil in liquid form after planting. *Cyperus conglomeratus* plants were fertilized with 20 % the amount of nutritional elements provided to Sudan grass plants. For both plants, the substrate in each cell was watered to approximately field capacity once per day using deionized water.

### 1.2.2 Set up of the field experiment

On the 10<sup>th</sup>, 11<sup>th</sup> and 12<sup>th</sup> of March-2015 Sudan grass and *C.conglomeratus* plantlets were transferred to the field.



The experimental field trial comprised of 20 plots, each measuring 1.75 x 1.4 m (Fig. 1). The plots were arranged in four rows of equal dimension. The distance between the five plots within the same row was 1 m, and between the rows 3 m. Each plot was equipped with six irrigation lines spaced 35 cm apart. Four plants were grown along each irrigation line at a distance of, again, 35 cm. Within each plot, five irrigation drippers were installed in each irrigation line. These were centered between the plants in a way that each plant had one irrigation dripper 17.5 cm to its left, and another at the same distance to its right. The plots were either planted only with Sudan grass SS, only with *C. conglomeratus* CC, or alternating rows of both plants SC. Of each plant species, 250 individuals of equal size were selected. Out of these, 240 were transferred to the experiment, while the remaining were kept in the cell trays. For transplanting, root bales were removed from the cell trays, and the plants were transferred to the field soil together with all growth substrate from the cell in which they had been precultivated. The ten remaining plants selected for the experiment were used to replace individuals that died within three weeks after transplanting into the field.

All plots were equipped with drippers releasing 8L of water per hour throughout the entire growth period. The intercropped plots were either also supplied exclusively via 8 L per hour drippers (+) Water, or had the 8 L per hour drippers replaced by 4 L per hour drippers later in the growth period (-) Water. Each plot constituted one experimental unit. There were five replicates of each of the four treatments. The treatments were distributed over the plots completely randomized.

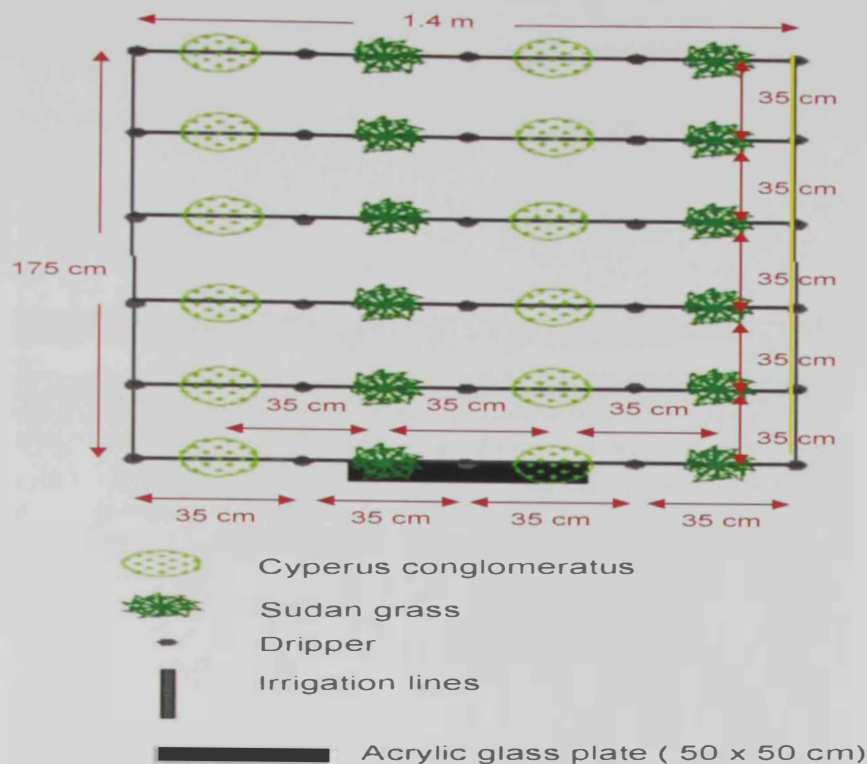


Figure 1: The distribution of the plants and drippers in one intercropped plot of the field experiment

1.2.3 Installation of a root monitoring window

Two weeks after planting, a window that would allow for the monitoring of root growth in the soil was installed at the narrow side of each plot. A hole of approximately 50 cm depth, 70 cm width, and 100 m length was dug into the ground at the place where the window was to be installed. A 1 cm thick acrylic glass plate (50 x 50 cm) was installed vertically against the side of the hole that was facing the planting rows (Fig. 2). The distance between the plants and the glass plate was between 10 and 15 cm. The glass plate was installed at a depth of 45 cm, so that it extended above the soil surface by around 5 cm. Two wooden bars were beaten into the ground to keep the root window in place. To keep the roots in the dark, and prevent the soil behind the

window from heating up, foam boards wrapped in aluminous foil were used to cover the glass plate, as well as the hole. The root window was divided into four 25 x 25 cm sections, labeled A (top left), B (top right), C (bottom left) and D (bottom right).



Figure 2: A root window made out of an acrylic glass Plate installed in the plot planted with *C.conglomeratus*

#### 1.2.4 Maintenance of the experiment in the field

The experiment was conducted at Al Foah Experimental Farm from March until October 2015. April to August with an average daily high temperature above 40 °C. However, the temperature in October is decreasing (Fig. 3).



Figure 3: The experiment site in the field at Al Foah Experimental Farm

Twenty-one days after transplanting, each Sudan grass plant of the field trial was supplied with 200 mg N ( $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ), 100 mg P ( $\text{KH}_2\text{PO}_4$ ), 200 mg K ( $\text{K}_2\text{SO}_4$ ), 100 mg Mg ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ), 10 mg Fe, 10 mg Zn, 7.5 mg Mn, 1.25 mg Cu, 3.75 mg B, 0.125 mg Mo (Multi-Micronutrient Fertilizer). Sudan grass plants of the SC and SS plots were fertilized with N, P, K, Mg, Fe, Zn, Mn, Cu, B and Mo at a rate of 19.05, 9.52, 19.05, 9.52, 0.95, 0.95, 0.71, 0.12, 0.36 and 0.01 kg per ha, respectively. *Cyperus conglomeratus* plants were supplied with half the amounts of nutrients provided to Sudan grass plants.

Thirty-six days after transplanting, each Sudan grass plant of the field trial was supplied with 200 mg N ( $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ), 20mg P ( $\text{KH}_2\text{PO}_4$ ), 200 mg K ( $\text{K}_2\text{SO}_4$ ), 100 mg Mg ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ), 25 mg Fe, 25 mg Zn, 18.75 mg Mn, 3.125 mg Cu, 9.375 mg B, 0.3125 mg Mo (Multi-Micronutrient Fertilizer). Sudan grass plants of the SC

and SS plots were fertilized with N, P, K, Mg, Fe, Zn, Mn, Cu, B and Mo at a rate of 19.05, 10.48, 19.05, 9.52, 2.38, 2.38, 1.79, 0.30, 0.89 and 0.02 kg per ha, respectively.

By 105 days after transplanting, each Sudan grass and *C. conglomeratus* of the field trial was supplied with 400 mg N ( $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ), 20 mg P ( $\text{KH}_2\text{PO}_4$ ), 300 mg K ( $\text{K}_2\text{SO}_4$ ), 100 mg Mg ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ), 15 mg Fe, 15 mg Zn, 11.25 mg Mn, 1.875 mg Cu, 5.625 mg B, 0.1875 mg Mo (Multi-Micronutrient Fertilizer) in mg between plants. Sudan grass and *C. conglomeratus* plants of the SC, SS and CC plots were fertilized with N, P, K, Mg, Fe, Zn, Mn, Cu, B and Mo at a rate of 38.10, 1.90, 30.25, 28.57, 9.52, 1.43, 1.43, 1.07, 0.18, 0.54 and 0.02 kg per ha, respectively.

The fertilizer application was done in liquid form, nutrient solution was poured over the soil at a distance of 1.5 cm from the base of the plant.

The young leaves and inflorescences of *C. conglomeratus* were occasionally colonized by aphids. Once this was observed, affected plant parts were cleaned with a washing powder solution (2 teaspoons per L of water). Sudan grass and *C. conglomeratus* were grown for seven months (Fig. 4), and were cut four times during the growth period to a height of 30 cm, 42, 70, 99 and 148 days after transplanting, respectively. All plant materials obtained by cutting were dried in paper bags in a drying oven at 65 °C for 48 h, then their dry weight were estimated.





Figure 4: Field experiment shortly before the final harvest

By 83 and 224 days after transplanting, the root samples were taken behind the root window. One sample was obtained from each of the four sections, A, B, C, D. After the acrylic glass plate had been carefully removed, a cork borer was horizontally driven into the ground in the middle of each section. The soil core obtained was 20 cm long and 2.5 cm in diameter (Fig. 5). At the same time the samples were taken, the soil behind the root windows was photographed, in order to perform root length measurements later on. The hole which was caused by the sampling was filled by wet field soil. The acrylic glass was cleaned, fixed and covered again. The soil samples were dried in a drying oven at 40 °C for four days.



Figure 5: Soil sample with roots by Cork borer (20 cm depth and 2.5 cm diameter)

The irrigation system was switched on twice per day, once in the morning and once in the afternoon, each time for 20 minutes. By 113 days after transplanting, the 8 L drippers of the (-) Water/SC plots were replaced by 4 L drippers. By 207 days after transplanting, the irrigatin time was decreased to 10 minutes at each interval. The amount of water was applied in (+) Water/plot per  $\text{m}^2$  of plot area in 206 days (50.76 L per  $\text{m}^2$  per day), in 28 days (25.43 L per  $\text{m}^2$  per day) and for all growth period (11.17  $\text{m}^3$  per  $\text{m}^2$  growth period). The amount of water was applied in (-) Water/SC plot per  $\text{m}^2$  of plot area in 112 days (50.76 L per  $\text{m}^2$  per day), in 94 days (25.43 L per  $\text{m}^2$  per day), in 28 days (12.66 L per  $\text{m}^2$  per day), for all growth period (8.43  $\text{m}^3$  per  $\text{m}^2$  growth period).

### 1.2.5 Harvest and dry weight

By 227 days after transplanting, the plants were harvested from the field. For the final harvest, aboveground biomass of each plant was cut to the ground level. Each plot was divided into four sections (Fig. 6). The two plants that had their roots observed through the window were considered section 'RW'. Section 'N' comprised of six plants neighboring the section 'RW'. The eight plants that had grown along the middle irrigation lines were considered section 'M', and section F comprised of the remaining eight plants that were grown along the two irrigation lines on the opposite side of the root window. For each plot, plants of the same species and from the same section were pooled together. The plant material was cut into small pieces, and the total fresh weight

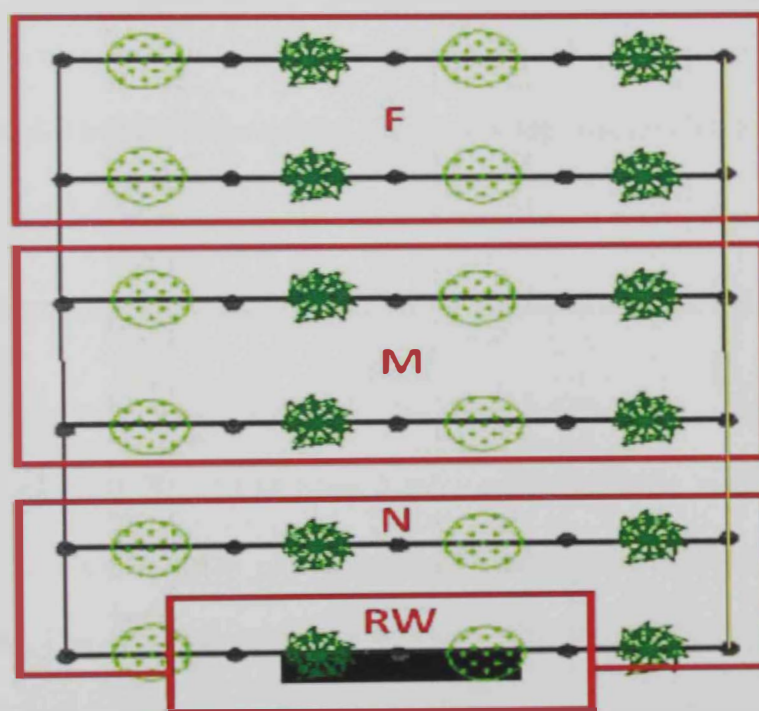


Figure 6: At the final harvest, plot was divided into four sections (RW, N, M, F)



was taken directly after the harvest. A representative subsample of the fresh material was then taken (around 100 g), and dried in paper bags in a drying oven at 65 °C for 48 h. then the dry weight of the subsample was estimated. the water content of the fresh biomass was calculated.

After drying the sample was obtained from each of the four sections. A, B, C, D. the rhizosheath and root were separated and the rhizosheath weight was taken. then the rhizosheath and root were washed and dried in a drying oven at 65 °C for 24 hours. their dry weight of them was taken. the weight of rhizosheath in percentage total root was calculated. The extent of mycorrhizal root colonization for Sudan grass root was assessed by the procedure of Vierheilig et al. (1998). washed the roots, put the roots in KOH or NaOH (10 % weight) for 25 minutes at 65 °C, washed with tap water, put it in vinegar for 2 to 3 minutes. then in hot Ink (50 ml ink + 1 L Vinegar) for 5 to 7 minutes and the last step was putting it in tap water with a few drops of vinegar.

#### **1.2.6 Analysis of the plant material for element concentrations and contents**

For mineral element analysis, the dry plant material was ground into powder using a hammer mill. The CEM Mars 5 microwave digestion system was used to extract the elements from the plants' samples (Brand name CEM, Model Mars5, Origin USA). The digestion procedure was according to the USEPA method 3015A guidelines (USEPA, 1998). This microwave digestion method was designed to mimic extraction using conventional heating with concentrated nitric acid (HNO<sub>3</sub>) and hydrochloric acid (HCl).

The plants' samples were prepared by weighing 0.25 to 0.30 g of sample into each microwave digestion vessel, and adding 10 ml of concentrated nitric acid ( $\text{HNO}_3$ ) and 2 ml hydrochloric acid ( $\text{HCl}$ ). The vessels were capped and placed into the microwave digestion system. After heating the samples at 1600 W for 20 min (final temperature 220 °C), they were transferred into graduated containers and brought to a volume of 50 ml with deionized water.

Concentrations of macro- and microelements (P, K, Mg, Ca, Na, Fe, Cu, Zn and Mn) in the liquid samples were measured using Inductively coupled plasma optical emission spectroscopy (ICP\_OES) Model 710-ES, Varian, United States. The element concentrations in the plant material were calculated by referring the measured concentrations to the amount of the plant material that was digested. Shoot element contents (g per plant) at the time of harvest were calculated by multiplying the element concentrations (g per kg plant material) by the amount of dry weight (in Kg) obtained from the corresponding plants.

### 1.2.7 Statistical analysis

Data obtained for treatment replicates was averaged, and the standard deviation was calculated. Data obtained for (+) Water plants was analyzed by a Two Way ANOVA, with the first factor being the identity of the plant species for which the data was obtained, and the second factor being the identity of the respective neighboring plant species. Another Two Way ANOVA was performed on data obtained for the SC treatments under (+) or (-) Water supply, testing whether the identity of the plant species or the water supply level had a significant ( $P < 0.05$ ) effect on the mean values. To test whether individual mean values differed significantly ( $P < 0.05$ ) from each

other, Tukey's multiple comparison was performed. Statistical analyses were performed using the SigmaStat 2.03 programme.

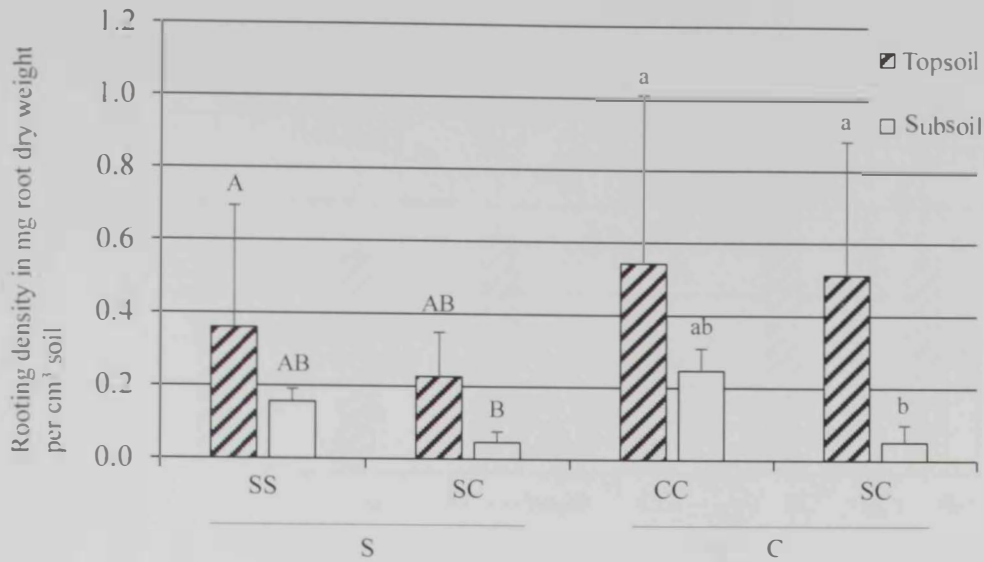
## 1.3 Results

### 1.3.1 Rooting density beneath *C. conglomeratus* and Sudan grass plants

At 83 days after transplanting soil samples taken from sections A and B (topsoil) did not differ in the root dry weight obtained per volume of soil depending on the treatment (Fig. 7). The subsoil (sections C and D) beneath *C. conglomeratus* plants appeared to be slightly better rooted compared with soil sampled below Sudan grass. Intercropping of both plant species had a negative effect on the rooting density in the subsoil, irrespective of whether samples were taken from beneath *C. conglomeratus* or Sudan grass.

The rooting density in the topsoil approximately doubled between 83 and 224 days after transplanting in all treatments. Rooting densities in the subsoil also increased with time. In the sole cropped plots there was no difference in rooting density in the topsoil and the subsoil depending on the plant species at 224 days after transplanting (Fig.8). When the plants were intercropped, the rooting density in topsoil sampled beneath *C. conglomeratus* plants was slightly higher compared with topsoil sampled from CC plots. Beneath Sudan grass plants there was no difference in rooting density depending on whether plants were sole cropped or intercropped. The water supply level had no effect on the rooting density in the topsoil or subsoil beneath intercropped plants.

The rooting densities in the topsoil were generally at least two times higher compared with those in the subsoil. Neither at 83 nor at 224 days after transplanting did treatments differ in the relative distribution of roots between topsoil and subsoil (data not shown).



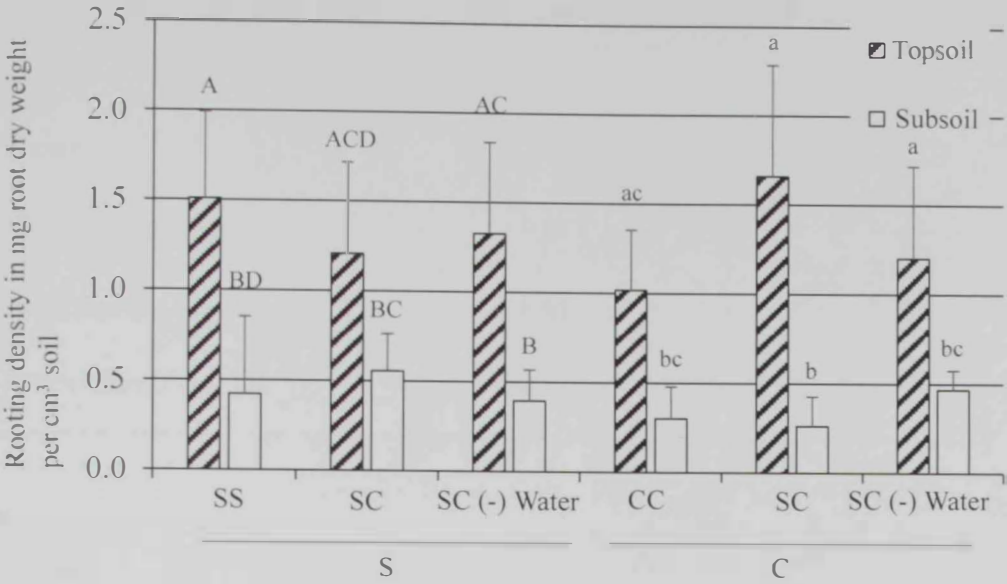
### Topsoil

Factor	P-Value
Plant species (Sp)	0.071
Neighboring species (N)	0.681
Interaction (Sp x N)	0.518

### Subsoil

Factor	P-Value
Plant species (Sp)	<b>0.009</b>
Neighboring species (N)	<b>0.015</b>
Interaction (Sp x N)	<b>&lt; 0.001</b>

Figure 7: Rooting densities measured 83 DAP (in mg root dry weight per cm<sup>3</sup> soil). The values are the means  $\pm$  standard deviation for soil samples obtained from beneath Sudan grass (S) or *C. conglomeratus* (C) plants, either sole cropped (SS / CC), or intercropped (SC). The water supply treatments were not yet established at 83 DAP, and thus values obtained for all ten (SC) plots were averaged. The table below the figure shows the results of the Two Way ANOVA. P-values indicating a significant ( $P < 0.05$ ) effect of the plant species (Sp), identity of the neighboring species (N), or a significant interaction between both factors are printed in bold. Mean values obtained were compared by Tukey's multiple comparison for the Sudan grass (capital letters) and the *C. conglomeratus* (small letters) separately. Mean values followed by the same letter are not significantly ( $P < 0.05$ ; Tukey's multiple comparison) different.



Results of the Two Way ANOVA performed on data obtained for SC plots of the (+) Water and (-) Water treatments:

Topsoil

Factor	P-Value
Plant species (Sp)	0.505
Water (W)	0.493
Interaction (Sp x W)	0.252

Subsoil

Factor	P-Value
Plant species (Sp)	0.160
Water (W)	0.764
Interaction (Sp x W)	<b>0.026</b>



Results of the Two Way ANOVA performed on data obtained for the (+) Water plots:

Topsoil

Factor	P-Value
Plant species (Sp)	0.937
Neighboring species (N)	<b>0.050</b>
Interaction (Sp x N)	0.454

Subsoil

Factor	P-Value
Plant species (Sp)	0.103
Neighboring species (N)	0.482
Interaction (Sp x N)	0.699

Figure 8: Rooting densities measured 224 DAP (in mg root dry weight per cm<sup>3</sup> soil). The values are the means ± standard deviation. For treatment abbreviations see Fig. 7. The tables below the figure show the results of the Two Way ANOVAS performed on the data obtained for the SC plots under different irrigation water supply levels (top), or on all (+) Water treatments (bottom). P-values indicating a significant ( $P < 0.05$ ) effect of the plant species (Sp), identity of the neighboring species (N), Water (W) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. Mean values obtained were compared by Tukey's multiple comparison for the Sudan grass (capital letters) and the *C. conglomeratus* (small letters) separately. Mean values followed by the same letter are not significantly ( $P < 0.05$ ; Tukey's multiple comparison) different.

White roots with dense coats of root hairs were occasionally observed beneath all *C. conglomeratus* plants through the root windows (Fig. 9). Such rhizosheaths were also formed in the subsoil (sections C and D). Most *C. conglomeratus* roots, however, appeared to be of brown coloration and without root hairs (Fig. 10). Visual appraisal did not reveal differences in rhizosheath formation beneath *C. conglomeratus*

between the treatments. No rhizosheaths were observed beneath sole cropped Sudan grass plants.

At 83 days after transplanting soil samples taken from sections A and B (topsoil) did not differ in the average of rhizosheath in percentage of the total root depending on the treatment (Table 1). Intercropping had a negative effect in the average of rhizosheath in percentage of the total root in the subsoil for the samples were taken from beneath *C. conglomeratus*. The average of rhizosheath in percentage of the total root in the topsoil and subsoil at 224 days after transplanting was lower than the average at 83 days after transplanting and did not differ depending on the treatment.



Figure 9: White roots with dense coats of root hairs were observed beneath *C. conglomeratus* plants through the root windows





Figure 10: Typical brownish *C. conglomeratus* roots

Table 1: The weight of rhizosheath in percentage of the total root measured 83 DAP and 224 days after planting (DAP).

		S			C		
		SS	SC	SC (-) Water	CC	SC	SC (-) Water
Topsoil	83 DAP	0.00	13.51	*	8.70	14.45	*
		±0.00	±22.43		±9.09	±19.87	
	224 DAP	0.00	2.36	5.42	0.03	4.86	6.00
		±0.00	±5.28	±8.59	±0.07	±7.47	±8.52
Subsoil	83 DAP	0.54	16.60	*	21.52	5.44	*
		±1.21	±25.95		±21.14	±11.79	
	224 DAP	0.49	0.00	25.17	0.00	2.36	8.13
		±1.09	±0.00	±34.47	±0.00	±5.28	±11.15

Topsoil

Factor	P-Value
Plant species (Sp)	0.495
Neighboring species (N)	0.582
Interaction (Sp x N)	0.179

Subsoil

Factor	P-Value
Plant species (Sp)	0.641
Neighboring species (N)	<b>0.016</b>
Interaction (Sp x N)	0.811

The values are the means ± standard deviation. For treatment abbreviations see Fig. 7. The water supply treatments were not yet established at 83 DAP (\*), and thus values obtained for all ten SC plots were averaged. The table below the Table 1 shows the results of the Two Way ANOVA at 83 DAP. P-values indicating a significant ( $P < 0.05$ ) effect of the plant species (Sp), identity of the neighboring species (N), or a significant interaction between both factors are printed in bold.

### 1.3.2 Formation of aboveground biomass

The cumulative total shoot dry weight obtained by cutting the plant shoots back to a height of 30 cm (done four times throughout the growth period: 42, 70, 99, and 148 days after transplanting) did not differ depending on whether the plots were SS, CC or SC (Fig. 11). The shoot dry weight obtained at 42 days after transplanting was below 15 g in most plots. At the final harvest SS plot had lower shoot dry weight compared to CC plot.

When the aboveground dry weight production of the individual plant species was observed, neither the water supply level, nor the identity of the neighboring plant had an effect (Fig. 12). At the time of the final harvest, the total dry weight produced by *C. conglomeratus* plants appeared to be slightly more than that of the Sudan grass.

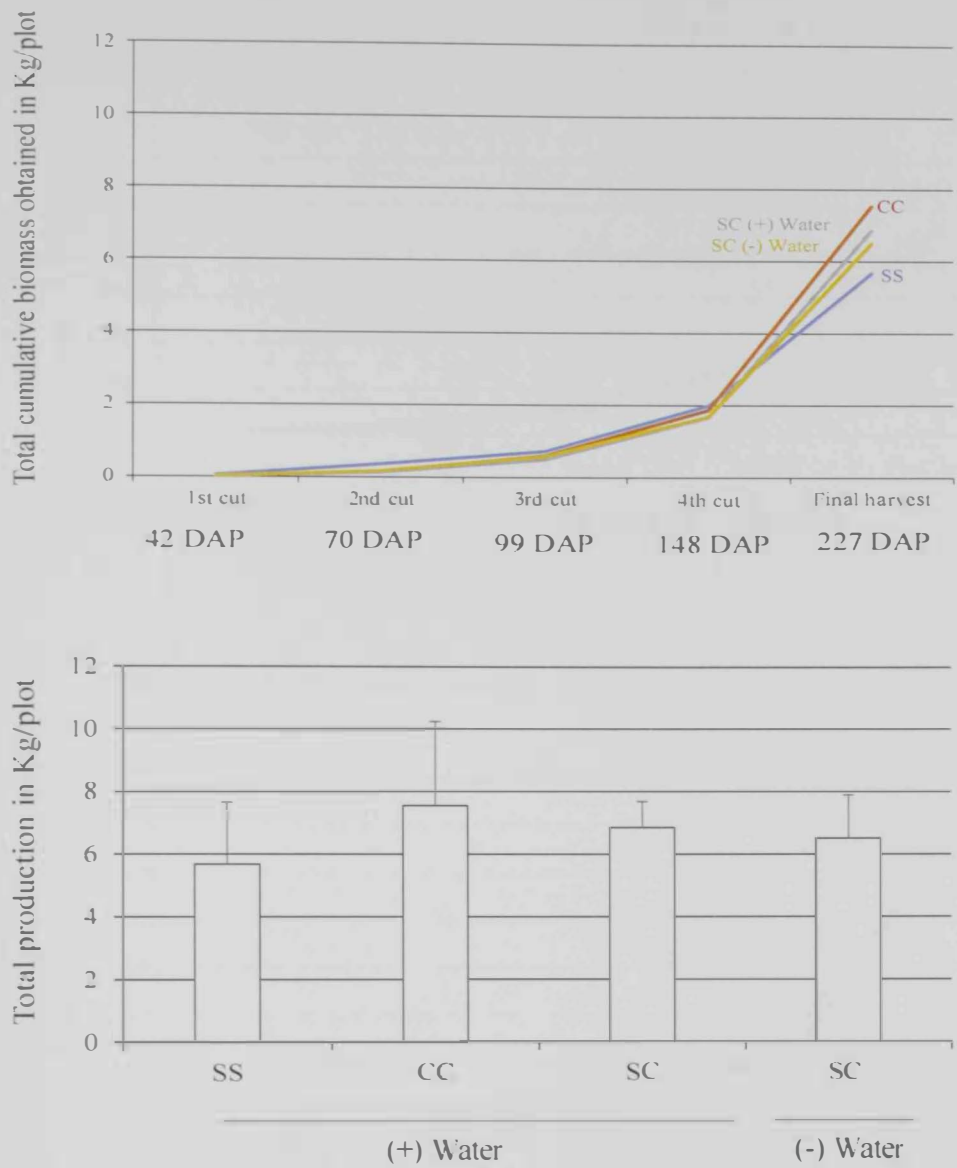
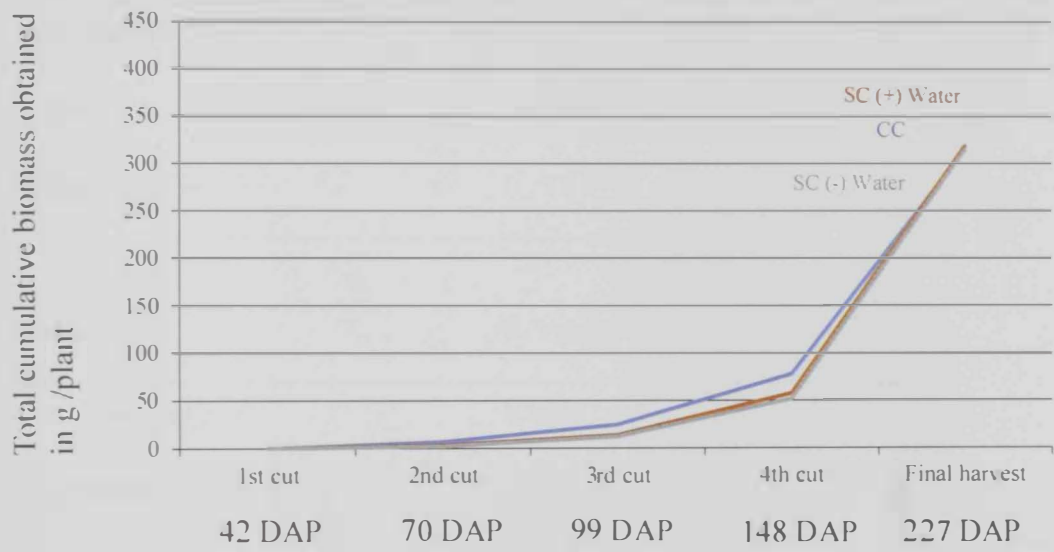
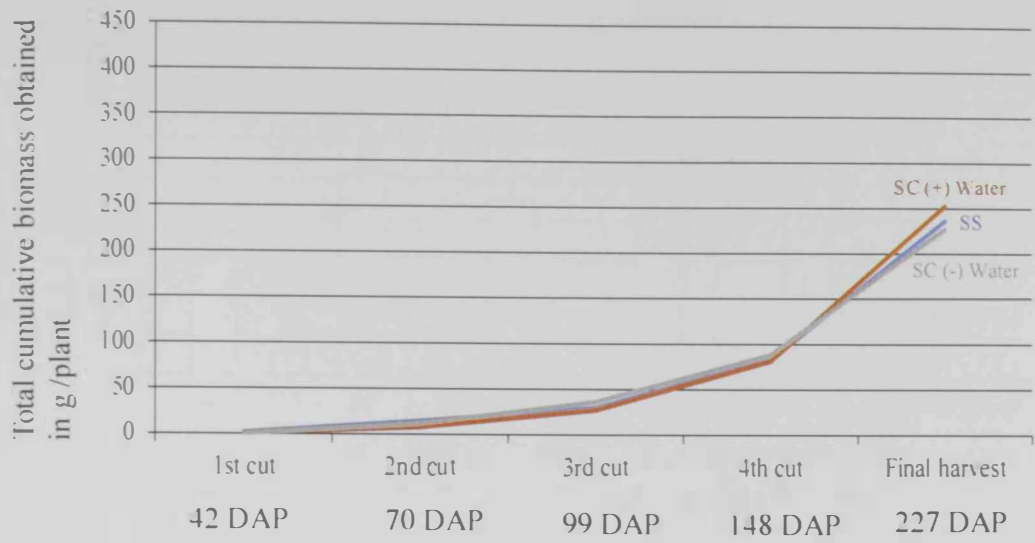
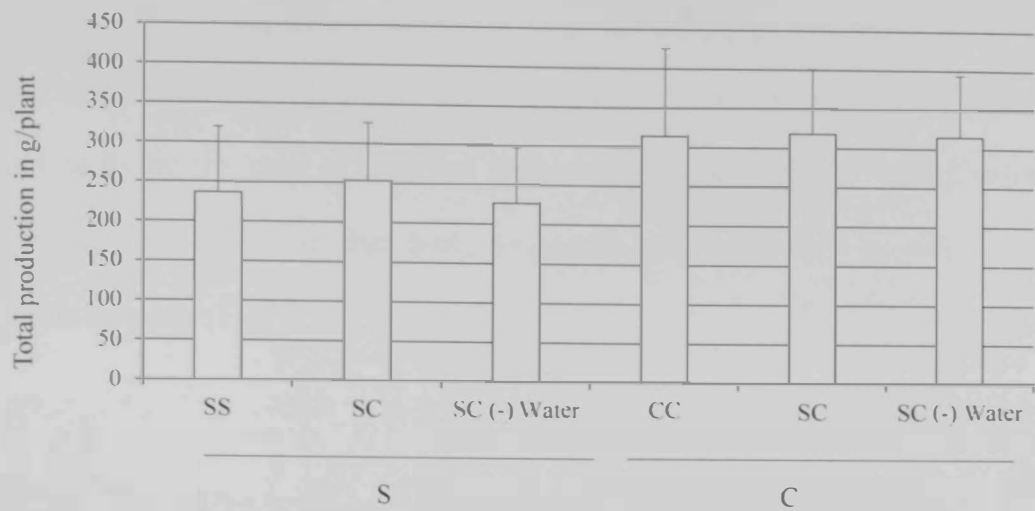


Figure 11: Total aboveground dry weight formed throughout the whole growth period in kg per plot. The upper graph shows the cumulative dry weights obtained by mowing shoots to a height of 30 cm for each mowing interval. The lower graph shows the total dry weight of all aboveground material obtained throughout the growth period. No significant difference was found between the mean values ( $P < 0.05$ , Tukey's multiple comparison).





Factor	P-Value
Plant species (Sp)	<b>0.039</b>
Water (W)	0.674
Interaction (Sp x W)	0.746

Factor	P-Value
Plant species (Sp)	0.090
Neighboring species (N)	0.881
Interaction (Sp x N)	0.800

Figure 12: Total aboveground dry weight formed throughout the whole growth period in g per plant. The upper first graph shows the cumulative dry weights obtained by mowing Sudan grass shoots to a height of 30 cm for each mowing interval and the second graph for *C. conglomeratus*. The lower graph shows the total dry weight of all aboveground material obtained throughout the growth period. The table below the figure shows the results of the Two Way ANOVAS performed on the data obtained for the SC plots under different irrigation water supply levels (top), or on all (+) Water treatments (bottom). P-values indicating a significant ( $P < 0.05$ ) effect of the plant species (Sp), identity of the neighboring species (N), Water (W) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. The mean values did not significantly differ ( $P < 0.05$ ; Tukey's multiple comparison).



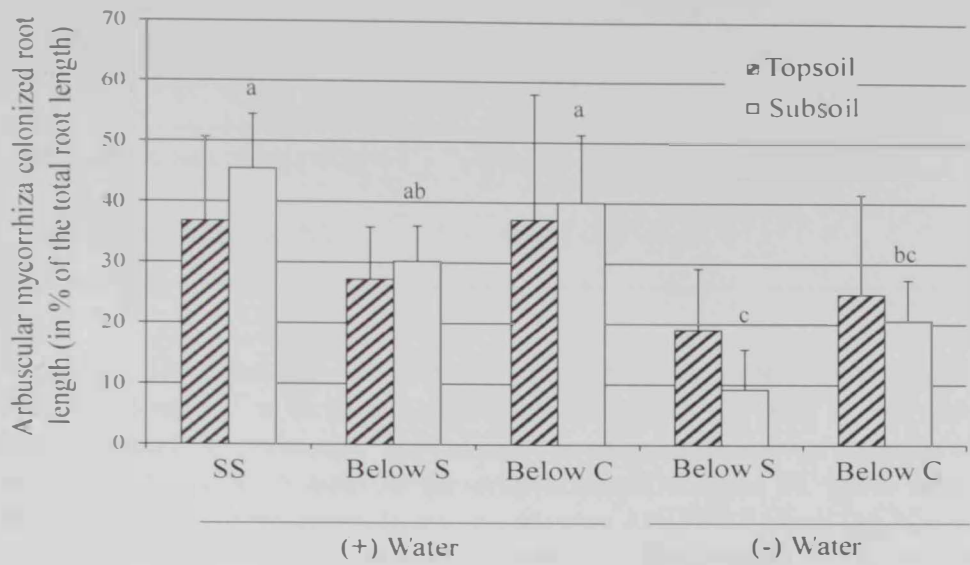
Both, *C. conglomeratus* and Sudan grass entered the generative stage between one and three months after transplanting. Plants of all treatments had formed flowers and seeds by the time of the final harvest. Both plant species were continuously forming new tillers, so that both, vegetative and generative growth took place simultaneously (Fig. 13).



Figure 13: Plants in the field shortly before the final harvest

### 1.3.3 Arbuscular mycorrhiza fungal root colonization

The extent of mycorrhiza fungal root colonization did not differ depending on the soil depth (Fig. 14). Decreased water supply towards the end of the growth period had a negative effect on the extent of endomycorrhiza root colonization in SC treatments, irrespective of whether roots were sampled beneath Sudan grass or *C. conglomeratus*. In SC treatments, roots sampled beneath *C. conglomeratus* showed a higher extent of arbuscular mycorrhiza fungal root colonization compared with roots sampled beneath Sudan grass.



Results of the Three Way ANOVA performed on data obtained for SC plots of the (+) Water and (-) Water treatments:

Factor	P-Value
Soil depth	0.603
Water (W)	<0.001
Plant species (Sp)	0.026

Results of the Two Way ANOVA performed on data obtained for the (+) Water plots:

Topsoil

Factor	P-Value
Plant above sampling point	0.968
Neighboring species (N)	0.340



Subsoil

Factor	P-Value
Plant above sampling point	0.373
Neighboring species (N)	<b>0.031</b>

Figure 14: The arbuscular mycorrhiza fungal colonized root length in percent of the total root length. For treatment abbreviations see Figs. 7 and 8. The values are the means ± standard deviation. The tables below the figure show the results of the Three Way ANOVAS performed on the data obtained for the SC plots under different irrigation water supply levels (top), or Two way ANOVAS on all (+) Water treatments (bottom). P-values indicating a significant ( $P < 0.05$ ) effect of the soil depth, plant species (Sp), water (W), Plant above sampling point, identity of the neighboring species (N) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. Mean values obtained were compared by Tukey's multiple comparison for the topsoil and the subsoil separately. Mean values followed by the same letter are not significantly ( $P < 0.05$ ; Tukey's multiple comparison) different. For the topsoil, the mean values did not significantly differ.

1.3.4 Element analysis

The shoot concentrations of P, K, Ca and Na were considerably higher for *C. conglomeratus* compared with Sudan grass (Tables 2, 3 and 4). Concentrations of Mg were also slightly higher in shoots of *C. conglomeratus*. The Two Way ANOVA did not reveal an effect of the identity of the neighboring plant species or the water supply level on macronutrient concentrations in plant shoots. Patterns of micronutrient concentrations in shoots differed considerably between the two plant species tested in this experiment. While shoot Fe concentrations were nearly twice as high in *C. conglomeratus* compared with those in Sudan grass, the latter had much higher Zn and Mn concentrations. Cu concentrations were also slightly higher in shoots of Sudan grass.

Table 2: Element concentrations in shoot material obtained from Sudan grass and *C. conglomeratus* plants at the time of the final harvest.

	S			C		
	SS	SC	SC (-) Water	CC	SC	SC (-) Water
P (mg per g DW)	1.63 ±0.18	1.68 ±0.14	1.77 ±0.27	2.47 ±0.48	2.28 ±0.78	1.90 ±0.48
K (mg per g DW)	6.76 ±0.52 b	6.72 ±0.62 b	7.02 ±0.51 b	11.87 ±0.77 a	10.61 ±1.24 a	10.60 ±0.93 a
Mg (mg per g DW)	3.37 ±0.32	3.41 ±0.12	3.74 ±0.60	3.61 ±0.34	3.84 ±0.30	3.71 ±0.42
Ca (mg per g DW)	6.92 ±0.90	5.89 ±0.53	7.23 ±2.10	8.61 ±1.27	8.24 ±1.62	8.56 ±0.88
Na (mg per g DW)	0.20 ±0.08 b	0.15 ±0.05 b	0.19 ±0.05 b	2.65 ±0.60 a	2.04 ±0.79 a	2.62 ±0.41 a
Fe (µg per g DW)	252.17 ±62.77 bc	215.45 ±28.86 c	283.18 ±162.33 ac	450.58 ±100.29 ac	470.87 ±145.60 ab	490.84 ±114.56 a
Cu (µg per g DW)	2.56 ±0.25 ab	2.80 ±0.36 ab	2.44 ±0.31 a	2.10 ±0.31 b	2.24 ±0.28 ab	2.19 ±0.30 ab
Zn (µg per g DW)	45.33 ±3.06 a	45.25 ±11.80 a	54.16 ±11.95 a	7.78 ±1.47 b	9.33 ±2.92 b	8.00 ±0.70 b
Mn (µg per g DW)	49.02 ±15.78 ab	51.58 ±13.73 ab	65.54 ±17.24 a	38.42 ±5.11 b	45.29 ±1.86 ab	45.42 ±2.03 ab

The values are the means ± standard deviations in mg per g dry weight (DW) for macronutrients, and in µg per g DW for micronutrients. For treatment abbreviations see Fig. 7. Mean values followed by the same letter are not significantly ( $P < 0.05$ ; Tukey's multiple comparison) different. The mean values (P, Mg and Ca) did not significantly differ ( $P < 0.05$ ; Tukey's multiple comparison).

Table 3: Results of the Two Way ANOVA performed on data obtained for average element concentrations in the shoots of plants of the SC plots under (+) Water or (–) Water supply.

	ANOVA			
	Sp		W	
	P-Value	F-Value	P-Value	F-Value
P	0.124	2.676	0.518	0.440
K	<b>&lt;0.001</b>	84.592	0.729	0.124
Mg	0.327	1.031	0.605	0.280
Ca	<b>0.018</b>	7.170	0.246	1.469
Na	<b>&lt;0.001</b>	113.588	0.146	2.372
Fe	<b>0.002</b>	14.892	0.477	0.534
Cu	<b>0.015</b>	7.625	0.183	1.962
Zn	<b>&lt;0.001</b>	103.143	0.365	0.878
Mn	<b>0.027</b>	6.090	0.209	1.731

For treatment abbreviations see Fig. 7. P values indicative of a significant ( $P < 0.05$ ) influence of the plant species (Sp), or the water supply level (W) are printed in bold. There were no significant interactions between the two factors (data not shown).

Table 4: Results of the Two Way ANOVA performed on data obtained for average element concentrations in the shoots of plants of the SS, CC or SC plots under (+) Water supply.

	ANOVA			
	Sp		N	
	P-Value	F-Value	P-Value	F-Value
P	<b>0.005</b>	10.946	0.582	0.318
K	<b>&lt;0.001</b>	136.070	0.137	2.488
Mg	<b>0.030</b>	5.834	0.521	0.433
Ca	<b>0.002</b>	13.855	0.545	0.385
Na	<b>&lt;0.001</b>	88.092	0.248	1.451
Fe	<b>&lt;0.001</b>	26.241	0.530	0.414
Cu	<b>0.003</b>	12.801	0.732	0.122
Zn	<b>&lt;0.001</b>	171.604	0.776	0.0842
Mn	0.126	2.647	0.685	0.172

For treatment abbreviations see Fig. 7. P values indicative of a significant ( $P < 0.05$ ) influence of the plant species (Sp), or the neighboring species (N) are printed in bold. There were no significant interactions between the two factors (data not shown).

*Cyperus conglomeratus* plants had higher amounts of P, K, Mg, Ca, Na and Fe in their shoots compared with those in Sudan grass by the time of the final harvest (Tables 5, 6 and 7). The shoot Zn content, however, was higher for Sudan grass compared to *C. conglomeratus*. Both plant species had equal amounts of Cu and Mn in their shoots by the time of the final harvest. Intercropped plants did not differ from corresponding sole cropped treatments in their shoot element content. The latter also remained unaffected by the water supply regime.

Table 5: Element content in shoot biomass obtained from Sudan grass and *C. conglomeratus* plants at the time of the final harvest.

	S			C		
	SS	SC	SC (-) Water	CC	SC	SC (-) Water
P (mg per plant)	251.62 ±95.44 b	300.70 ±66.73 ab	251.32 ±132.90 b	548.66 ±142.69 a	535.94 ±250.79 ab	471.89 ±108.46 ab
K (g per plant)	1.02 ±0.30 c	1.22 ±0.34 bc	0.95 ±0.27 c	2.78 ±1.02 a	2.47 ±0.70 ab	2.71 ±0.73 a
Mg (g per plant)	0.51 ±0.15 b	0.61 ±0.15 ab	0.51 ±0.17 b	0.85 ±0.30 ab	0.89 ±0.22 ab	0.95 ±0.24 a
Ca (g per plant)	1.04 ±0.31 bd	1.05 ±0.19 bcd	0.95 ±0.25 d	1.93 ±0.56 ac	1.93 ±0.66 ab	2.18 ±0.54 a
Na (mg per plant)	27.94 ±6.73 b	25.59 ±6.71 b	26.26 ±10.28 b	637.08 ±259.01 a	469.98 ±183.91 a	662.67 ±152.44 a
Fe (mg per plant)	37.10 ±9.56 c	38.39 ±8.55 bc	35.79 ±14.47 c	100.16 ±31.75 ab	112.01 ±51.36 a	125.94 ±41.43 a
Cu (mg per plant)	0.39 ±0.12	0.50 ±0.13	0.34 ±0.14	0.47 ±0.13	0.51 ±0.08	0.55 ±0.13
Zn (mg per plant)	6.89 ±2.24 a	7.89 ±1.87 a	7.47 ±3.28 a	1.72 ±0.43 b	2.13 ±0.67 b	2.02 ±0.35 b
Mn (mg per plant)	6.98 ±1.41	9.35 ±3.44	8.45 ±0.87	8.91 ±3.28	10.45 ±2.38	11.65 ±3.22

The values are the means ± standard deviations in mg per plant or in g per plant for macronutrients, and micronutrients. For treatment abbreviations see Fig. 7. Mean values followed by the same letter are not significantly ( $P < 0.05$ ; Tukey's multiple comparison) different. The mean values (Cu and Mn) did not significantly differ ( $P < 0.05$ ; Tukey's multiple comparison).

Table 6: Results of the Two Way ANOVA performed on data obtained for total element content in the shoots of plants of the SC plots under (+) Water or (–) Water supply.

	ANOVA			
	Sp		W	
	P-Value	F-Value	P-Value	F-Value
P	<b>0.007</b>	10 108	0.442	0.626
K	<b>&lt;0.001</b>	32.918	0.970	0.00151
Mg	<b>0.002</b>	14.166	0.815	0.0569
Ca	<b>&lt;0.001</b>	24.587	0.713	0.141
Na	<b>&lt;0.001</b>	93.191	0.106	2.983
Fe	<b>&lt;0.001</b>	26.350	0.728	0.126
Cu	0.079	3.587	0.327	1.033
Zn	<b>&lt;0.001</b>	35.285	0.780	0.0809
Mn	0.107	2.975	0.905	0.0147

For treatment abbreviations see Fig. 7. P values indicative of a significant ( $P < 0.05$ ) influence of the plant species (Sp), or the water supply level (W) are printed in bold. There were no significant interactions between the two factors (data not shown).

Table 7: Results of the Two Way ANOVA performed on data obtained for total element content in the shoots of plants of the SS, CC or SC plots under (+) Water supply.

	ANOVA			
	Sp		N	
	P-Value	F-Value	P-Value	F-Value
P	<b>0.002</b>	13.776	0.673	0.186
K	<b>&lt;0.001</b>	22.215	0.429	0.662
Mg	<b>0.010</b>	8.796	0.744	0.111
Ca	<b>0.001</b>	15.857	0.977	0.001
Na	<b>&lt;0.001</b>	46.646	0.304	1.141
Fe	<b>&lt;0.001</b>	23.197	0.715	0.139
Cu	0.441	0.628	0.520	0.435
Zn	<b>&lt;0.001</b>	57.067	0.688	0.168
Mn	0.259	1.382	0.751	0.105

For treatment abbreviations see Fig. 7. P values indicative of a significant ( $P < 0.05$ ) influence of the plant species (Sp), or the neighboring species (N) are printed in bold. There were no significant interactions between the two factors (data not shown).



## 1.4 Discussion

### 1.4.1 Growth and dry matter yield of intercropped versus sole cropped Sudan grass or *C. conglomeratus*

Due to their high drought tolerance, as well as water and nutrient use efficiencies, species of the genus *Sorghum* are often grown for biomass production on soils that are not ideally suitable for the cultivation of more demanding crops such as corn or rapeseed (Gardner et al., 1994). Maximum yields of *Sorghum bicolor* and Sudan grass have been reported to require N fertilization levels of 200 kg per ha, or more (Collett, 2004; Almodares et al., 2007; Propheter et al., 2010). However, economically feasible production of *S. bicolor* biomass has also been achieved at fertilization levels between 60 and 180 kg per ha in some studies (Hallam et al., 2001; Houx and Fritschi, 2013). Compared with these results, amounts of N applied to Sudan grass plants of this study (74 kg per ha) were in a rather low supply range. Application rates of phosphate (13.7 kg per ha) and potassium (69 kg per ha) were in an intermediate to low range compared with values commonly recommended for Sorghum or Sudan grass (Pal et al., 1982; Collett, 2004).

Fertilization requirements for *C. conglomeratus* are not known. Some wild plants adapted to very low soil nutrient availabilities have been shown to respond with growth depression or death to levels of mineral fertilizers normally supplied to crops (Lambers et al., 2013). Thus, relatively low amounts of N (38.10 kg per ha), P (1.90 kg per ha) and K (30.25 kg per ha) were supplied to *C. conglomeratus* in the present experiment.



According to the UNEP (1992), the potential evapotranspiration in the area of the UAE lies between 2000 to 2400 mm per year. Annual pan evaporation was estimated to be 3322 mm per year in the area of Al Dhayd in 1993/94 (JICA, 1996). Compared with these values, Irrigation water supplied to the field plots in the present experiment was in a high range, even for the (-) Water treatments. However, it needs to be considered that the plants of the present study were not cut as frequently as commercial pastures. Thus, the plants had a relatively high standing biomass throughout the growth period, which may have required large quantities of water during the hot season. *Sorghum bicolor* L. Moench can tolerate moderate or even severe water deficits. Compared with other fodder grasses, it has been shown to produce higher above-ground biomass, and exhibit higher water use efficiency under water deficit in previous studies (Farre and Faci, 2006; Sutka et al., 2016).

According to personal observations, farmers in the UAE commonly grow Sudan grass at planting densities of 2 – 4 plants per m<sup>2</sup>. This is lower than the planting density of 9.8 plants per m<sup>2</sup> established in the present study. Under favorable soil conditions, maximum *S. bicolor* yields have been achieved at planting densities more than two times higher than the ones established in the present study (May et al., 2016). Godsey et al. (2012) came to the conclusion that a wide range of planting densities would be acceptable for *S. bicolor*, given the ability of the plants to tiller. A planting density of 8.5 per m<sup>2</sup> has been proposed as optimal by Thomas et al. (1980).

In the present study sole cropped Sudan grass plots produced on an average 23.02 ton dry matter per ha throughout the growth period. A maximum *S. bicolor* yield was 14,250 kg dry matter per ha per year at the high planting density 836 plants per ha (Fischer and Wilson, 1975). This is lower than the yield in the present study. Berenguer

and Faci (2001) concluded that high planting densities do not always result in higher yields of *S. bicolor*.

Irrespective of whether plants were solecropped or intercropped, *C. conglomeratus* produced higher biomass compared with Sudan grass in the present study, even though it received much lower amounts of fertilizer. This suggests that *C. conglomeratus* had a higher fertilizer exploitation efficiency compared with Sudan grass.

At 83 days after transplanting the rooting density in the subsoil was lower beneath both, Sudan grass and *C. conglomeratus* when the plants were intercropped, compared with corresponding sole cropped treatments. At 224 days after transplanting, this difference was no longer apparent. Instead, a slightly higher rooting density was observed beneath intercropped compared with sole cropped *C. conglomeratus* of the (+) Water treatments. The aboveground plant biomass obtained throughout the growth period was not affected by the identity of the neighboring plant. There was also no effect of the neighboring plant species on total element contents. It seems that from these results, the plants were largely unaffected in their growth and nutrient uptake by the identity of the neighboring species.

Intercropping systems often achieve higher overall yields compared with sole cropping, because interspecific is often smaller than intraspecific competition, as different species have different resource requirements (Tilman, 1982; Aarssen, 1983; Spitters, 1983; Fowler, 1986; Goldberg and Barton, 1992). In the present experiment aboveground yields of neither plant species were different depending on whether the plants were sole cropped or intercropped.

The intercropped plots received more fertilizer in total compared with the sole cropped *C. conglomeratus* plots. Sudan grass took up smaller quantities of nutritional elements compared with *C. conglomeratus*. Why did the *C. conglomeratus* plants that grew with Sudan grass not benefit from this in terms of better growth and nutrient uptake compared with plants that grew with another *C. conglomeratus*? It is possible that in the present experiment aboveground growth of plants was limited by factors that the plants did not compete for. Eventually, *C. conglomeratus* and Sudan grass did not compete for nutritional elements, because they exploited different nutrient pools. The results of the rooting density measurements do not suggest major differences in growth patterns between the two species. Rooting densities seem to be similar beneath the two plant species, whether they are intercropped or sole cropped. Even the reduction in root growth observed in intercropped compared with sole cropped plants at 83 days after transplanting is observed in both, Sudan grass as well as *C. conglomeratus*.

Results of the present experiment suggest that plant dry weight production depended on the season and related climatic conditions. Between 42 until 148 days after transplanting approximately there were no differences between treatments in plant biomass production, and this period ranged from April to August with an average daily maximum temperature above 40 °C. Compared with this, the plant biomass production increased between 148 and 227 days after transplanting. This might have been because the temperature in October is decreasing. Tilman (1988) and Brooker, (2006) reported that the nutrient availability and climate can also affect competitive interactions between plants. The strong growth increase towards the end of the growth period could also be the result of the third fertilization. Compared with what was

provided earlier, the third application was at a pretty high level, particularly for *C. conglomeratus*.

#### **1.4.2 Possible reasons for differences in nutrient acquisition between Sudan grass and *C. conglomeratus***

In this study, *C. conglomeratus* had higher contents of P, K, Mg, Ca, and Fe in the shoot compared to Sudan grass, even though the native plants were fertilized with smaller amounts of nutritional elements. This suggests that *C. conglomeratus* had access to nutrient pools not accessible to Sudan grass. The results of the root dry weight distribution analysis do not indicate major differences in rooting pattern between the two plant species. Though differences in horizontal root expansion or root length per g root dry weight can not be excluded, it is likely that the plants differed in their ability to mobilize nutritional elements in the rhizosphere.

There are several mechanisms used by plants to adapt under limited P availability and to enhance P acquisition such as: architecture modification of root growth (Barber, 1995; Lynch, 1995; Lynch and Brown, 2001) so, the root can explore more soil volume for P acquisition (Yu et al., 2012), acidification of rhizosphere (Neumann and Romheld, 1999; Hinsinger et al., 2003), exudation of carboxylates (Jones, 1998; Neumann and Romheld, 1999) and phosphatases (Helal, 1990).

In slightly sodic soils, such as those of the UAE, a relatively high proportion of P in the soil can be unavailable to plants, as it is bound into water insoluble calcium phosphates. Thus, even on soils fertilized with P, plants may not have access to adequate amounts of this element (Hinsinger, 2001; Richardson, 2001). The ability of the roots to mobilize and take up P from sparingly soluble sources differs depending

on the plant species. Soil moisture also has an important impact on P availability to plants. Also, plant supply with other nutritional elements can affect the P availability to plants.

Morphological and physiological characteristics of roots are often related to the plant P mobilization strategy. In the present study, shoots of Sudan grass and *C. conglomeratus* had P concentrations indicative of P deficiency. Concentrations were lower for Sudan grass compared with those for *C. conglomeratus*. It is possible that rhizosheaths helped *C. conglomeratus* plants to mobilize P from the soil. In the present experiment, the *C. conglomeratus* plants also had higher P contents in their shoots compared with Sudan grass.

It can not be excluded that rhizosphere acidification played a role in *C. conglomeratus* nutrient uptake. Abraho et al. (2014) provide evidence for considerable release of carboxylic acid from roots of non mycotrophic rhizosheath forming cactus. Shane et al., (2006) even propose that rhizosheath forming roots of sedges are functionally equivalent to cluster roots of the Proteaceae, which exploit soil P resources through release of large amounts of citrate. Rhizosheath forming plants might either release protons or organic acids themselves, or they host P mobilizing rhizobacteria around their roots. Iron concentrations in the tissues of both, Sudan grass and *C. conglomeratus* point to a rather high availability of this element. Iron concentrations and contents are much higher in *C. conglomeratus* compared with Sudan grass, while Zn concentrations are much lower and indicate deficiency. Such imbalances in the micronutrient supply observed in *C. conglomeratus* might also be the result of rhizosphere acidification, which mobilizes not only P, but also metal cations (Rengel, 2015). Previous studies have also shown that rhizosheath support Mn

mobilization and uptake in neutral and alkaline soils (Uren, 1993). Other studies found that rhizosheaths can have high concentrations of Fe (Wei et al., 2011). These findings were supported also in the current experiment with respect to the *C. conglomeratus* shoots.

On soils with a low P availability, P uptake by plants increases with increasing P absorbing surface of the root (Vilela and Anghinoni, 1984). Under P deficiency, root growth is increased in relation with that of the shoot. To increase the nutrient absorbing surface, plants often form more root hairs, or increase the length and density of lateral roots and root hairs (Foehse and Jungk, 1983; Gahoonia et al., 2001). Under P limitation, a high root length density is helping plants to maintain adequate uptake of P (Marschener, 1998; Linkohr et al., 2002). Yan et al. (2011) and Yu et al. (2012) reported that plants under P deficiency like maize formed thin roots with diameter less than 0.6 mm and their P use efficiency increased. In general, the root length and surface area are important factors to achieve a greater P-uptake under P-deficiency (Hinsinger et al., 2011; White et al., 2013; Fernandes et al., 2014). Efficiency of P acquisition under the field conditions depended on the development of the root system, and the root elongation rate (Barber, 1995; Hinsinger et al., 2011). Arbuscular mycorrhiza fungal root colonization is also believed to constitute a strategy by which the spatial availability of P is increased. Plant species that are non-hosts to mycorrhizal fungi are sometimes characterized by profusely branched root systems that provide a high density of fine roots for nutrient absorption. However, the results of this study do not suggest that *C. conglomeratus* formed more or finer roots than Sudan grass. This might support the hypothesis that in *C. conglomeratus* chemical rather than spatial availability of P was higher compared with Sudan grass. In *C. conglomeratus* additional nutrient absorptive area might have been provided by root hairs though.



In the current experiment, the good supply of Ca content in the *C. conglomeratus* that was more than that in Sudan grass may enhanced P availability. That happen by solubilization of Ca phosphates in the rhizosphere (Devau et al., 2010).

As nitrogen concentrations in plant material were not analyzed, no clear interpretation of the plant N nutritional status is possible. However, while Sudan grass plants showed clear symptoms of N deficiency by the time of the final harvest, the *C. conglomeratus* plants did not, even though they were larger. Either these plants had a higher internal N use efficiency or they acquired N more efficiently than Sudan grass. This might have been through N fixation of bacterial in the rhizosphere (Amaresan et al., 2014). In both cases this might lead to a higher photosynthetic capacity of *C. conglomeratus*, and thus a better ability to support nutrient uptake.

Apart from P and N, rhizosheaths may also facilitate uptake of other nutritional elements (Wei et al., 2011). In addition to a possible chemical mobilization, the rhizosheaths might support nutrient uptake via providing a high root hair density (Bailey and Scholes, 1997). The root hairs which are formed within the rhizosheaths are important for nutrients uptake such as:  $\text{Ca}^{2+}$ ,  $\text{K}^{+}$ ,  $\text{NH}_4^{+}$ ,  $\text{NO}_3^{-}$ ,  $\text{Mn}^{2+}$ ,  $\text{Zn}^{2+}$ ,  $\text{Cl}^{-}$  and  $\text{H}_2\text{PO}_4^{-}$ , as they increase their spatial availability (Yu et al., 2012). Root hairs increase the nutrient absorbing surface of the root, which is an advantage for the uptake of nutrients that have a low mobility in the soil solution, such as P (Peterson and Farquhar, 1996),  $\text{NH}_4^{+}$  and micronutrients. Contribution to the uptake of  $\text{NO}_3^{-}$  or  $\text{K}^{+}$  is most likely rather low.

The Zn content was lower in the shoots of *C. conglomeratus* compared to that in Sudan grass. It is possible that the arbuscular mycorrhizal root colonization contributed to Zn uptake in Sudan grass plants, as has been reported previously (Ortas,



2003; Koide and Mosse, 2004; Ortas, 2009; Hart and Forsythe, 2012). But, it is also possible that uptake of Zn was lower in *C. conglomeratus* because of excessive availability of Fe, due to rhizosphere mobilization processes. The fungus can contribute to nutrient uptake in plants, but it does not entirely control it. Mycorrhizal fungi can assist the plant absorption of microelements (Turk et al., 2006; van der Heijden et al., 2006).

In the present study the plant species with the mycorrhiza strategy was apparently less successful in terms of nutrient uptake compared with the non-host. Maybe the roots of Sudan grass were not colonized sufficiently, or an increase in the nutrient absorbing surface provided by the mycorrhiza fungal symbiosis was not very efficient without additional chemical mobilization taking place.

Comparing the element concentrations in the shoot with optimum values cited by Loop (1983) and Bergmann (1992) for *Sorghum vulgare*, it can be concluded that, tissue concentrations of P, K, Cu in Sudan grass and *C. conglomeratus* shoots and Zn in *C. conglomeratus* shoots were indicative of deficiency. All the Sudan grass and *C. conglomeratus* showed enough and good supply of Mg, Ca and Mn concentrations in their shoots as well as Zn concentration in the Sudan grass.

Comparing the element concentration of Na in the shoot with maximum threshold limits of Na cited by Kirkby (1992) for Sudan grass, it can be concluded that, tissue concentrations of Na in Sudan grass and *C. conglomeratus* shoots were less than the maximum threshold limits of Na. Results show much higher uptake of Na into *C. conglomeratus* shoots compared with that in Sudan grass. Though soil Na availability was not elevated in the present experiment, it is possible that mycorrhizal fungi helped to decrease Na concentrations in the shoots of Sudan grass by reducing the uptake of

Na compared with the non-host *C. conglomeratus*. Some studies reported that host plant Na uptake can be enhanced by arbuscular mycorrhiza fungal root colonization (Allen and Cunningham, 1983). In contrast, Sharifi et al. (2007) and Zuccarini and Okurowska (2008) suggested that the Na levels can be lower in mycorrhizal compared with nonmycorrhizal plants. Mechanisms by which mycorrhizal fungi prevent host plants from uptake of Na are not completely understood. Most studies on this topic have been done on plants that grew on soils with excessive Na availability, which was not the case in the present study. For example, Allen and Cunningham (1983) suggested that the buffering effect on the uptake of Na by mycorrhizal root colonization had an influence on the uptake of Na by host plants. Also, the arbuscular mycorrhiza mycelia might retain Na in the fungal structures, and thus reduce Na availability to hosts (Cantrell and Linderman, 2001). It could also be speculated that the K uptake system is less selective for K in *C. conglomeratus*. In most plants, Na is taken up via the K uptake system.

#### **1.4.3 The effect of irrigation water supply on plant growth and nutrient uptake**

The availability of nutrients decreases when roots are exposed to dry soil, because diffusion and mass flow of nutritional elements decrease. Excessive irrigation could also decrease nutrient availability, as it may lead to nitrate leaching (Han et al., 1995; Cambouris et al., 2008; Jégo et al., 2008; Alva et al., 2012; Giletto and Echeverria, 2013; Poch-Massegú et al., 2014). With increasing irrigation water application rates (Shock et al., 2013; Wolie et al., 2016), as well as extending irrigation intervals (Wolie et al., 2016), nitrate leaching increases. Under excessive irrigation, potassium might also leach out of the rooting zone. The highest nutrient exploitation levels and crop yields are obtained under optimal water supply (Alva, 2004; Zebarth

and Rosen, 2007). A negative effect on yield can be caused by excessive as well as deficient water supply (Goffart et al., 2011). Saeed and El-Nadi, (1998) found that trickle irrigation for a short interval increased the dry matter yield of *S. bicolor* compared with non-irrigated controls. This study also reported that the additional irrigation can cause stem elongation and increase the yield of sorghum. In the current study, differences in nutrient uptake or growth were not observed between the irrigation treatments, suggesting that neither growth nor nutrient availability were different between the treatments. Reasons could be that the (-) Water treatment was also supplied with sufficient amounts of irrigation water, or that the period during which water supply was reduced was too short.

#### **1.4.4 The effect of water supply, and sole- versus intercropping on the extent of arbuscular mycorrhiza fungal root colonization**

In the present study, roots sampled beneath *C. conglomeratus* plants were mycorrhiza colonized to a higher extent compared with roots sampled beneath Sudan grass in the SC treatments. The reasons for this remain speculative. It can not be completely excluded that eventually *C. conglomeratus* roots might have become mycorrhiza (surface) colonized in the presence of an actively growing mycorrhiza hyphal network. Given the complete absence of mycorrhiza fungal structures in sole cropped *C. conglomeratus*, this is not very likely, but reports of non-hosts becoming surface colonized under high inoculum pressure exist. Veiga et al. (2013) reported that the arbuscular mycorrhizal fungi reduce growth and infect roots of the non-host plant *Arabidopsis thaliana*. Mycorrhiza colonization often increases with decreasing nutrient availability to the plant (Treseder & Vitousek, 2001). Most likely nutrient availability was lower beneath *C. conglomeratus* compared with Sudan grass plants.

first because these plants took up more nutrients, and second because they received less fertilizers. Another possibility is that rooting patterns of the plants were in a way that both, Sudan grass and *C. conglomeratus* formed a larger number of roots beneath the stem of the respective neighboring plant, compared with beneath their own stem. This would have resulted in a relatively larger number of roots of Sudan grass being sampled beneath *C. conglomeratus*, and vice versa.

The endomycorrhiza fungal root colonization decreased when the water supply decreased. Relatively much water was supplied to the plants of the (+) Water treatment, and this might have caused greater leaching of nutrients from the soil in (+) Water compared with (-) Water treatments, and thus lower nutrient availability in (+) Water treatments. However, there were no differences in nutrient acquisition between the (-) Water and (+) water treatments, and thus this is not a very likely possibility. Less irrigation might have resulted in higher soil temperature, and thus less mycorrhizal root colonization. Another possibility is that water limitation reduced photosynthesis, and thus carbon supply to the fungal symbiont during the last weeks of the growth period (Paul and Kucey, 1981). On the other hand, a decreased photosynthesis would possibly have been reflected in poorer growth of the (-) Water plants as well. This was, however, not observed.

## Chapter 2: Comparative study of phosphorus acquisition between Sudan grass and *Cyperus conglomeratus*

### 2.1 Introduction

Almost all agricultural soils of the UAE are slightly sodic with pH values between 7.5 and 8.5. Under these conditions, P that is applied to the soil in soluble form reacts with  $\text{Ca}^{2+}$  and  $\text{OH}^-$  to form water-insoluble calcium phosphates. These are sparingly available to plants. The concentration of P in the soil solution is thus often very low, even when phosphate fertilizers are applied.

Plants have evolved various strategies to facilitate P uptake from soils with a low P availability. These often involve an increase in the nutrient absorptive surface area of the root, e.g. via the formation of long and dense root hairs (Foehse and Jungk, 1983; Gahoonia et al., 2001), or the association with mycorrhizal fungi (Smith et al., 2011). The extraradical mycorrhiza fungal hyphal network can increase the nutrient absorptive surface area of the host plant considerably (Li et al., 1991a). Hyphae have much smaller diameters than roots, and can thus access soil pores that can not be penetrated by roots (Smith et al., 2011). Root colonization by mycorrhizal fungi has also sometimes been observed to trigger the formation of a larger plant root system (Sharif and Claassen, 2011).

Some plants have also evolved strategies by which phosphate can be chemically mobilized from sparingly soluble sources such as calcium phosphates. These involve the release of organic acids (Marschner, 1998) and  $\text{H}^+$  into the rhizosphere (Liu et al., 2004).

More than 80 % of all land plants form mycorrhizal associations. Sudan grass is a species known to associate with arbuscular mycorrhizal fungi in the formation of endomycorrhizal symbioses. While almost all members of the Poaceae are thought to be mycotrophic, the Cyperaceae comprise numerous non-host species to mycorrhizal fungi (Muthukumar et al., 2004). It could be speculated that rhizosheaths like those formed by *C. conglomeratus* also play a major role in the acquisition of P from desert sodic soils.

However, the precise functioning of rhizosheaths is not yet completely understood. The observation that rhizosheaths comprise of a dense coat of root hairs (Bristow et al., 1985) may suggest a role in facilitating the uptake of nutritional elements by increasing the nutrient absorptive surface area.

Rhizosheath formation has also been observed to involve the attachment of soil particles to root hairs and the root surface by means of mucilage (Chaboud, 1983; Watt et al., 1993; Read and Gregory, 1997). This may support the ability of the plant to modify chemical properties of the rhizosphere soil, such as its pH. Rhizosheaths have also been shown to support rhizosphere colonization by potentially beneficial microorganisms, such as bacteria with nitrogen fixing capabilities (Watt et al., 1994; Amellal et al., 1998; Bergmann et al., 2009).

To exploit their full phosphate uptake potential, mycotrophic plants rely on the presence of propagules of functionally compatible mycorrhizal fungi in the soil (Jansa et al., 2005; Javot et al. 2007). Thus, on soils where such propagules are present in insufficient amount or quality, a non-mycotrophic strategy may be of advantage. Desert soils from where plants are largely absent, and which are subject to extreme temperature and erosion, may not contain sufficient amounts of mycorrhiza fungal



propagules to establish fully functional symbioses within one or two growing seasons. In the field trial described in Chapter 1, Sudan grass showed a lower shoot uptake of P and other macronutrients compared with *C. conglomeratus*. It can not be excluded that this was due to the relatively low rate of arbuscular mycorrhiza fungal root colonization, and/or association with functionally not well compatible mycorrhiza fungal strains. Though the mycotrophic grasses that had been cultivated on this field site before might have fostered the establishment of mycorrhiza fungal hyphal networks and propagules in the soil, fungal infectivity might have decreased again in response to ploughing and keeping the land fallow for one year (Kabir, 2005).

The experiment described in the following aimed at further elucidating to which extent nutrient uptake from desert soils by mycotrophic Sudan grass and non-mycotrophic *C. conglomeratus* would depend on the presence of mycorrhiza fungal propagules in the growth substrate. Since the endomycorrhiza fungal symbiosis has most frequently been shown to contribute to plant P uptake, the focus of this study lay on this element. To test whether *C. conglomeratus* and Sudan grass would exploit the same or different pools of P in the soil.

Competition for phosphorus between two plant species was observed. To do this, plants were grown in three compartment split root pots in the greenhouse. These allowed for the study of P uptake from a soil compartment that was either shared between two individuals of the same, or of the different species. Competition for water and nutrients other than P was minimized.



## 2.2 Materials and Methods

### 2.2.1 Plant material and seedling preparation

*Cyperus conglomeratus* plants were collected from a naturally established plant stand along a roadside in Al Foah. Rhizome cuttings were cut approximately with same size and weight and the roots were folded with moist tissue until the time of planting into cell trays (Fig. 15). The same method as described in Chapter 1 was used for germination of Sudan grass seeds. *Cyperus conglomeratus* rhizome cuttings and Sudan grass seedlings were planted in cell trays on the 21<sup>st</sup> of April 2015.

Each cell was filled with 70 g of dry, sieved soil from an undisturbed sand dune near Al Foah, UAE, at a bulk density of  $1.6 \text{ g cm}^{-3}$ . For Sudan grass, the soil in each cell was fertilized with 200 mg N ( $\text{NH}_4\text{NO}_3$ ), 50 mg P ( $\text{KH}_2\text{PO}_4$ ), 100 mg K ( $\text{K}_2\text{SO}_4$ ), 100 mg Mg ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ), 20 mg Fe (Fe EDDHA), 15 mg Mn ( $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$ ) per kg dry soil in liquid form after planting. *Cyperus conglomeratus* plants were fertilized with 30 % the amount of nutritional elements provided to Sudan grass plants. For both plants, the substrate in each cell was watered to approximately field capacity once per day using deionized water.



Figure 15: *Cyperus conglomeratus* was propagated by rhizome cuttings

### 2.2.2 Planting pot and growth substrate preparation

Twenty-three days after planting in the cell trays, Sudan grass and *C. conglomeratus* were transplanted into three compartment split root pots. These comprised of a row of three square black plastic planting containers of equal size, fastened together with adhesive tape. Each of the planting containers had a total volume of 660 ml, and was filled with 1060 g of dry topsoil from a non-disturbed sand dune near Al Foah, UAE, at a bulk density of  $1.6 \text{ g cm}^{-3}$ . Prior to being used for filling the pots, the soil was sieved by 2 mm, and was heat sterilized for 7 h at  $85^\circ\text{C}$ .

The soil was further mixed with either freshly air-dried (mycorrhizal) or autoclaved (nonmycorrhizal) mycorrhiza inoculum at a rate of 8 % w/w. Topsoil from a 20 years old *Vachellia tortilis* and *Prosopis cineraria* plantation was used as inoculum. It consisted of a mixture of colonised root pieces from both species, and adhering air dried soil. The inoculum was also passed through a 2 mm sieve. Root pieces remaining on the sieve were cut into pieces of 1-2 cm length, and were added back to the sieved material. A quarter of the inoculums for the Non-Myc treatments was filtered two times with deionised water (2 L per 1 kg dry inoculum through Whatmann Filter paper) before being autoclaved at  $120^\circ\text{C}$  for 20 minutes. The remaining three quarters of dry inoculums for nonmycorrhizal treatments was sterilized at  $95^\circ\text{C}$  for 24 hours. The filtrate was added to the soil prepared for nonmycorrhizal plants to encourage a microflora similar to that of the [mycorrhizal]-treatments.

After mixing with inoculum, the soil for all three root compartments of each split root pot was fertilized with 100 mg N ( $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ), 200 mg K ( $\text{K}_2\text{SO}_4$ ), 100

mg Mg ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ), 20 mg Fe, 20 mg Zn, 15 mg Mn, 2.5 mg Cu, 7.25 mg B, 0.05 mg Mo (Multi-Micronutrient Fertilizer) per kg dry soil.

The soil for the central compartments received in addition 40 mg per kg P and 50 mg per kg K ( $\text{KH}_2\text{PO}_4$ ). To provide the soil in the outer compartments with the same amount of K as the inner one, additional 50 mg K ( $\text{K}_2\text{SO}_4$ ) was applied to the soil in these compartments.

For transplanting, Sudan grass and *C. conglomeratus* plants of approximately equal size were removed from the cell trays, and their roots were carefully washed free from adhering soil. The root system was split into two parts of approximately equal size. The plants were then grown with one part of their root system in the outer compartment, and another part in the middle one (Fig. 16). Either two *C. conglomeratus* CC, two Sudan grass SS, or one *C. conglomeratus* and one Sudan grass plant SC were transferred to each split root pot. The middle compartment was shared between two neighboring plants.

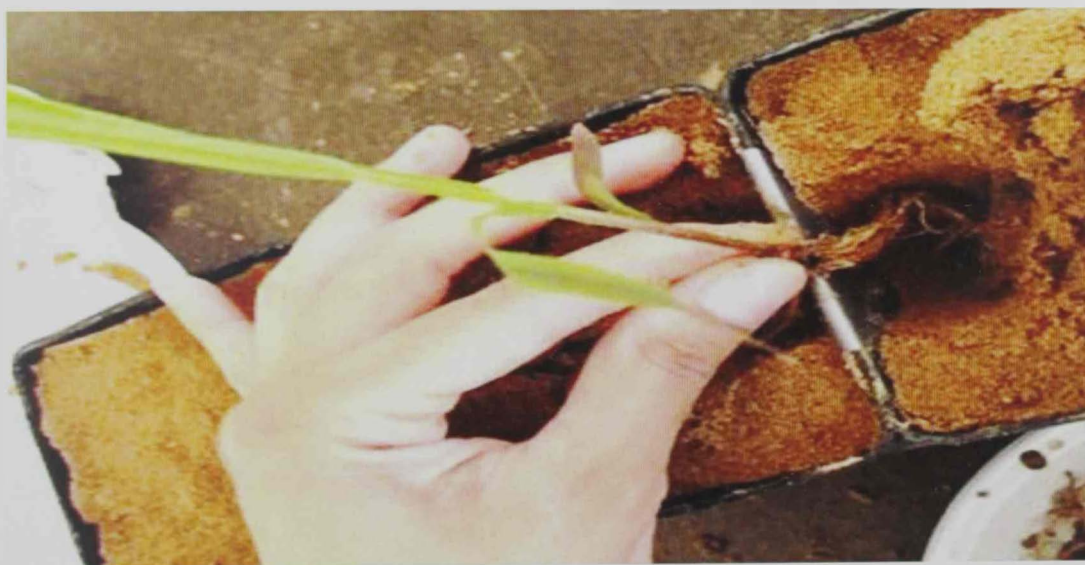


Figure 16: Sudan grass was transplanted as split root to triple planting pots

### 2.2.3 Maintenance of experiment in the greenhouse

The experiment was conducted in a greenhouse (tunnel type, polycarbonate cover, paved ground, 9 m x 36 m) at Al Foah Experimental Farm from 14<sup>th</sup> of May until 29<sup>th</sup> of September 2015. During May the temperature in the greenhouse was 22-23 °C during the day, and 16-18 °C during the night. From first of June until 29<sup>th</sup> of September it was 30 °C and 25-28 °C, respectively. The triple pots were set up completely randomized.

During the first two weeks after transplanting, the plants were covered with a transparent plastic bag to reduce evaporation (Fig. 17). Plants that did not survive the transfer to the split root pots within the first three weeks after transplanting were replaced.

Throughout the growth period, water loss from the triple pots was estimated gravimetrically every second day, and it was replaced with deionized water. After watering, the soil moisture level was approximately at field capacity. The distribution of irrigation water over the three compartments of each pot was done according to visual appraisal.

At approximately ten weeks after transplanting, Sudan grass plants entered the reproductive stage and began growing inflorescences. To foster tillering and maintain the plants in a vegetative stage, the flowers were cut off once they had fully emerged.

At 41 days after transplanting, the Sudan grass plants were fertilized with additional 200 mg N ( $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ), 100 mg K ( $\text{K}_2\text{SO}_4$ ), 10 mg Fe, 10 mg Zn, 7.5 mg Mn, 1.25 mg Cu, 3.75 mg B, 0.125 mg Mo (Multi-Micronutrient Fertilizer) per kg dry soil applied only to the outer compartment. At the same time, the shared



compartments were fertilized with 100 mg N ( $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ) and 20 mg P ( $\text{KH}_2\text{PO}_4$ ) per kg dry soil in all treatments. At 114 days after transplanting, the shared compartments were supplied with another 200 mg N per kg dry soil in form of  $\text{CO}(\text{NH}_2)_2$  per kg dry soil.



Figure 17: The three compartment split root pots in the greenhouse at 2 days after planting. The plastic bags were removed from *C. conglomeratus* 7 days after transplanting and from Sudan grass 14 days after transplanting

#### 2.2.4 Harvest and dry weight

The plants were harvested on the 20<sup>th</sup> of September-2015, at 131 days after planting. The shoots of all plants were cut off above the ground, and were then dried in paper bags in a drying oven at 65 °C for 48 h. The flowers cut from the Sudan grass plants during the growth period were added to the shoot material obtained at the terminal harvest. The soil in the root compartments was air dried, and then passed through a 2 mm and 1 mm sieve stacked upon one another. Root pieces were collected

by a forceps, and the loose adhering soil was gently shaken off. Soil that kept adhering to the roots was considered rhizosheath soil. The dry roots with the rhizosheath soil attached were weighed. The roots were then washed with tap water to remove any adhering material. Thereafter they were dried again at 65 °C for 48 h in a drying oven, and their dry weight was estimated.

### **2.2.5 Mycorrhiza root colonization**

Root samples for the assessment of the arbuscular mycorrhiza fungal colonized root length were taken at the time of final harvest. The samples were air dried, before they were spread on a plastic plate to pick out root pieces by a forceps.

The root samples were stained using blue ink (Flamingo; KM Stationery Industry, Thailand), and white vinegar with 4% acetic acid, using a method modified after Vierheilig et al. (1998). The root samples were first soaked with tap water for 5-10 minutes, and then cleared for 25 min. in a 10 % KOH or NaOH solution at 65 °C. They were then washed several times with tap water, and then placed into boiling vinegar containing 5 % vol/vol ink for 5-7 minutes. Until being observed, samples were stored in water with a few drops of vinegar added. The endomycorrhiza colonized root length was estimated using the grid line intersection method (Tennant, 1975; Kormanik and Mc Graw, 1982).

### **2.2.6 Analysis of the plant material for element concentrations and contents**

All shoot material formed by the plants throughout the growth period was ground to powder using a hammer mill, and was then analyzed for element concentrations. The same methods as described in Chapter 1 were used.

### 2.2.7 Statistical analysis

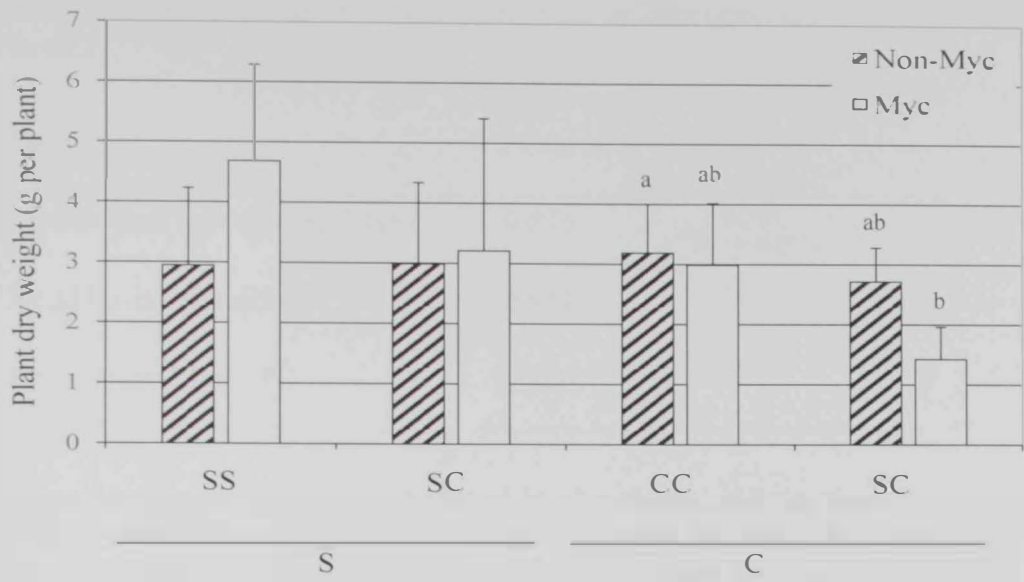
Data obtained for treatment replicates was averaged, and the standard deviation was calculated. For each of the two plant species data obtained was analyzed by a Two Way ANOVA testing whether there was a significant ( $P < 0.05$ ) effect of the identity of the respective neighboring plant, or mycorrhiza inoculation. To test whether individual mean values differed significantly ( $P < 0.05$ ) from each other, Tukey's multiple comparison was performed. Statistical analyses were performed using the SigmaStat 2.03 programme.



## 2.3 Results

### 2.3.1 Plant dry weight at the time of the terminal harvest

Mycorrhizal inoculation had no effect on the shoot dry weight of Sudan grass or *C. conglomeratus* plants (Fig. 18). When the soil was not inoculated with mycorrhiza propagules, both plant species had approximately the same shoot dry weight. There was also not a significant difference in shoot dry weight between plants of the SS and the CC treatment. However, when Sudan grass and *C. conglomeratus* shared the middle compartment, the presence of mycorrhiza inoculums reduced the shoot dry weight of *C. conglomeratus*.



Results of the Two Way ANOVA performed on data obtained for Sudan grass plants:

Factor	P-Value
Mycorrhizal inoculation (Myc)	0.288
Neighboring species (N)	0.431
Interaction (Myc x N)	0.404

Results of the Two Way ANOVA performed on data obtained for *C. conglomeratus* plants:

Factor	P-Value
Mycorrhizal inoculation (Myc)	0.076
Neighboring species (N)	<b>0.022</b>
Interaction (Myc x N)	0.180

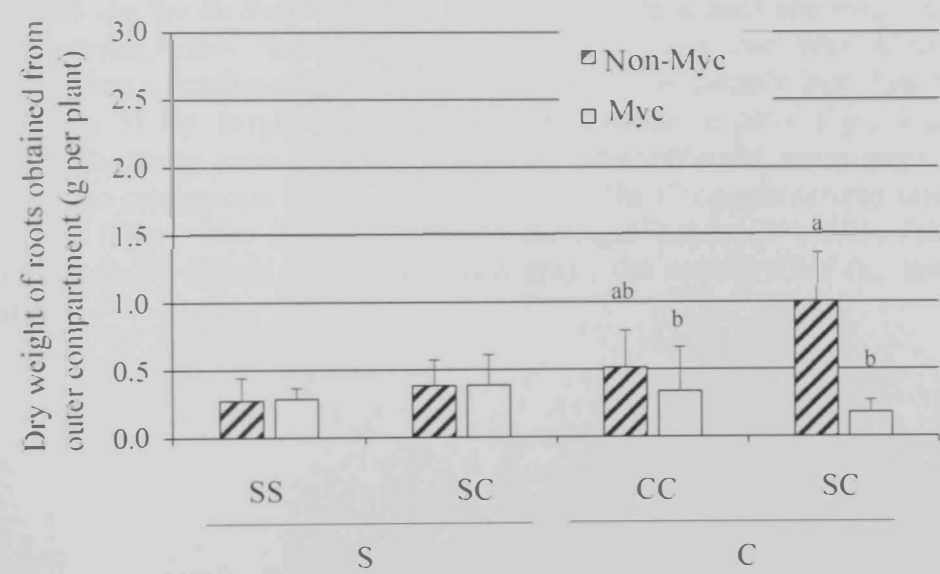
Figure 18: Shoot dry weight produced by the plants until the final harvest in g per plant. The values are the means  $\pm$  standard deviation for plants that were grown in the presence (Myc) or absence (Non-Myc) of mycorrhiza inoculum. Either two Sudan grass (SS), two *C. conglomeratus* (CC), or one plant of each species (SC) shared the middle compartment of a vertical three compartment split root pot with half of their root system. The tables below the figure show the results of the Two Way ANOVA. P-values indicating a significant ( $P < 0.05$ ) effect of mycorrhizal root inoculation (Myc) or the identity of the neighboring plant (N) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. Mean values obtained were compared by Tukey's multiple comparison for the Sudan grass and the *C. conglomeratus* separately. Mean values followed by the same letter are not significantly ( $P < 0.05$ ; Tukey's multiple comparison) different. For the Sudan grass, the mean values did not significantly differ.

It was originally planned to separate the *C. conglomeratus* and Sudan grass root parts that shared the middle compartment. However, since the roots of both plants were very fine and brittle, more than half of the roots got detached during the process of root extraction from soil, and could not be assigned to either of the plants. The roots obtained for the middle compartment were thus harvested, weighed and analysed together.

When the soil was nonmycorrhizal, *C. conglomeratus* produced a greater root biomass in the outer compartments compared with Sudan grass (Fig. 19). This effect was particularly pronounced when the neighboring plant was Sudan grass instead of another *C. conglomeratus*. There was no effect of the identity of the neighboring plant

on the dry weight of Sudan grass roots in the outer compartments. Mycorrhizal inoculation had also no effect on the dry weight of Sudan grass roots that grew alone. Mycorrhizal inoculation resulted in a reduction in *C. conglomeratus* root dry weight production in the outer compartments. This effect was particularly pronounced when the plants had Sudan grass as a neighbor.

While the amounts of roots formed in the outer compartments did not differ depending on the plant species, Sudan grass plants of the SS Treatment formed more roots in the central compartment compared with the CC plants (Fig. 20). The dry weight of roots obtained from the middle compartments shared between both species contained less roots compared with the SS, and more roots compared with the CC treatments. There was no effect of mycorrhiza inoculation on the amounts of roots formed in the middle compartment.



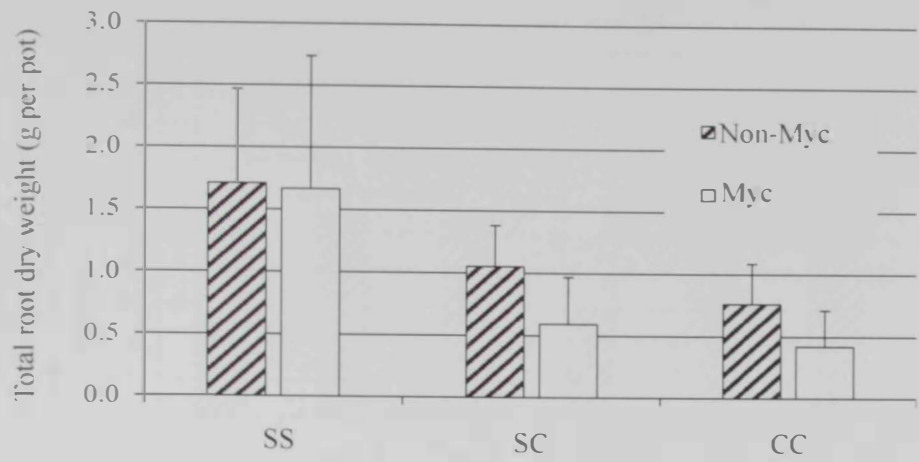
Results of the Two Way ANOVA performed on data obtained for Sudan grass plants:

Factor	P-Value
Mycorrhizal inoculation (Myc)	0.936
Neighboring species (N)	0.277
Interaction (Myc x N)	0.970

Results of the Two Way ANOVA performed on data obtained for *C. conglomeratus* plants:

Factor	P-Value
Mycorrhizal inoculation (Myc)	<b>0.006</b>
Neighboring species (N)	0.283
Interaction (Myc x N)	<b>0.047</b>

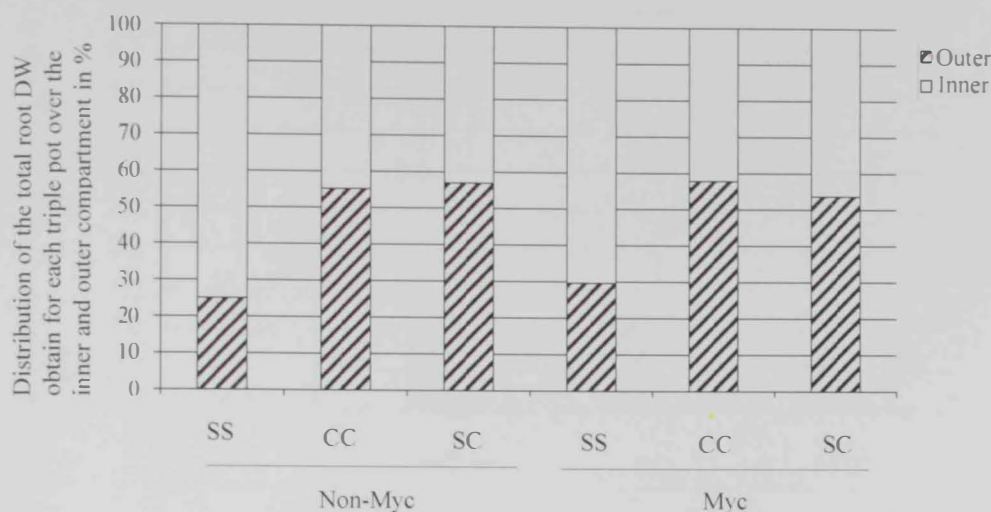
Figure 19: Dry weight of roots obtained from outer compartment in g per plant. The values are the means  $\pm$  standard deviation. For treatment abbreviations see Fig. 18. The tables below the figure show the results of the Two Way ANOVA. P-values indicating a significant ( $P < 0.05$ ) effect of mycorrhizal root inoculation (Myc) or the identity of the neighboring plant (N) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. Mean values obtained were compared by Tukey's multiple comparison for the Sudan grass and the *C. conglomeratus* separately. Mean values followed by the same letter are not significantly ( $P < 0.05$ ; Tukey's multiple comparison) different. For the Sudan grass, the mean values did not significantly differ.



Factor	P-Value
Plant species (Sp)	<b>0.009</b>
Mycorrhizal inoculation (Myc)	0.294
Interaction (Sp x Myc)	0.794

Figure 20: Root dry weight produced by the plants until the final harvest in g per pot in the shared pots. The values are the means  $\pm$  standard deviation. For treatment abbreviations see Fig. 18. The table below the figure shows the results of the Two Way ANOVA. P-values indicating a significant effect of mycorrhizal root inoculation (Myc) or the plant species combination (Sp) ( $P < 0.05$ ) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. The mean values did not significantly differ ( $P < 0.05$ ; Tukey's multiple comparison).

The distribution of roots over the outer and inner compartment was approximately equal for *C. conglomeratus* plants of the CC and SC treatments (Fig. 21). The SS treatment had relatively more root in the inner compartment than outer compartment irrespective of the mycorrhiza treatment.



Factor	P-Value
Plant species (Sp)	<b>0.027</b>
Mycorrhizal inoculation (Myc)	0.904
Interaction (Sp x Myc)	0.972

Figure 21: Distribution of the total root DW obtained for each triple pot over the inner and outer compartment in %. The values are the means. For treatment abbreviations see Fig. 18. The table below the figure shows the results of the Two Way ANOVA. P-values indicating a significant effect of mycorrhizal root inoculation (Myc) or the plant species combination (Sp) ( $P < 0.05$ ) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line.

The amount of dry soil attached to roots of Sudan grass and *C. conglomeratus* was between 1.1 - 2.5 g dry soil per g root dry weight, irrespective of whether the roots were extracted from the outer or the inner compartment (Figs. 22 and 23). The One Way ANOVA did not reveal a significant ( $P < 0.05$ ) effect of the identity of the plants on the amount of soil that was attached to the roots (statistics not shown). Mycorrhizal inoculation and neighbor had no effect on the amount of the soil attached to root (statistics not shown).



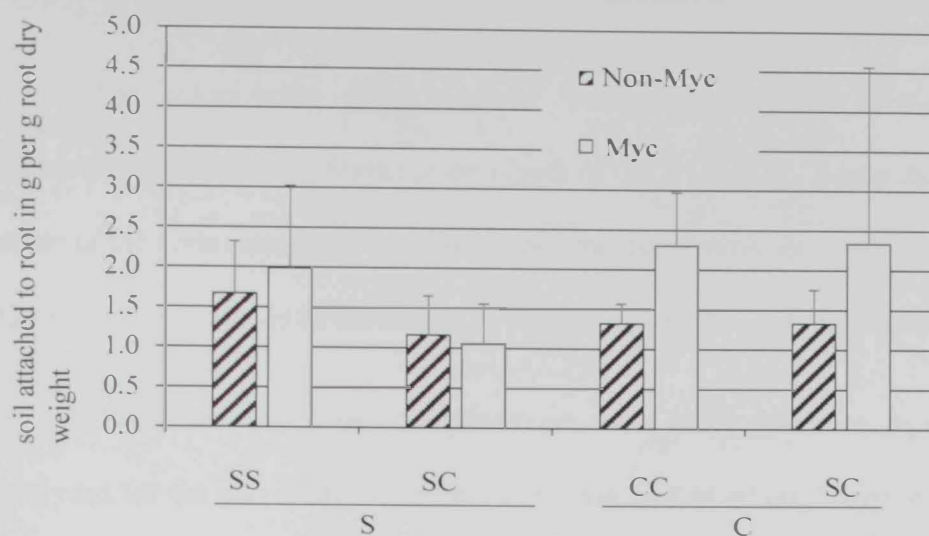


Figure 22: soil attached to the roots in g per g root dry weight in the outer pots. The values are the means  $\pm$  standard deviation. For treatment abbreviations see Fig. 18. Mean values obtained were compared by Tukey's multiple comparison for the Sudan grass and the *C. conglomeratus* separately. The mean values did not significantly differ ( $P < 0.05$ ; Tukey's multiple comparison).

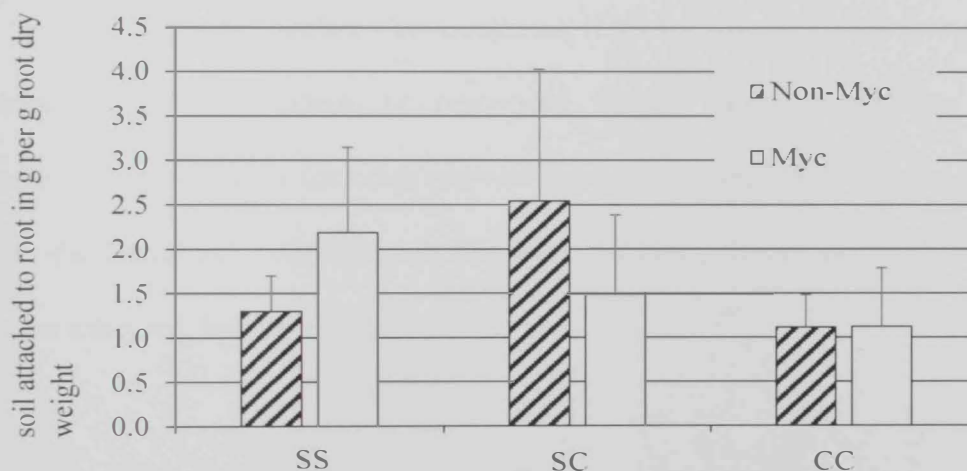


Figure 23: Soil attached to the roots in g per g root dry weight in the shared pots. The values are the means  $\pm$  standard deviation. For treatment abbreviations see Fig. 18. The mean values did not significantly differ ( $P < 0.05$ ; Tukey's multiple comparison).

### 2.3.2 Arbuscular mycorrhiza fungal root colonization

The colonization rates over the outer and the inner compartment was approximately equal for Sudan grass plants of the SS and SC treatments (Fig. 24). In some of the nonmycorrhizal treatments the amount of roots obtained was not sufficient to perform an analysis of the extent of mycorrhiza fungal root colonization.

Of the non-inoculated SS treatment, roots in all middle compartments were analyzed for the extent of mycorrhiza fungal root colonization. Three of these samples were found to be mycorrhiza colonized. The average extent of root colonization among these positive samples was  $19.75 \pm 13.80$  % of the total root length. Of the lateral SS compartments that were not mycorrhiza inoculated, six samples were analyzed, and two of them were positive for the presence of mycorrhizal fungi. These samples showed an average colonization rate of  $19.28 \pm 1.70$  % of the total root length.

Of the non-inoculated SC treatment, roots in two middle compartments were analyzed for the extent of mycorrhiza fungal root colonization. One was nonmycorrhizal, while the other one was colonized by 46.7 % of the total root length. Of the lateral SC compartments that were not mycorrhiza inoculated, two samples were analyzed, both were nonmycorrhizal.

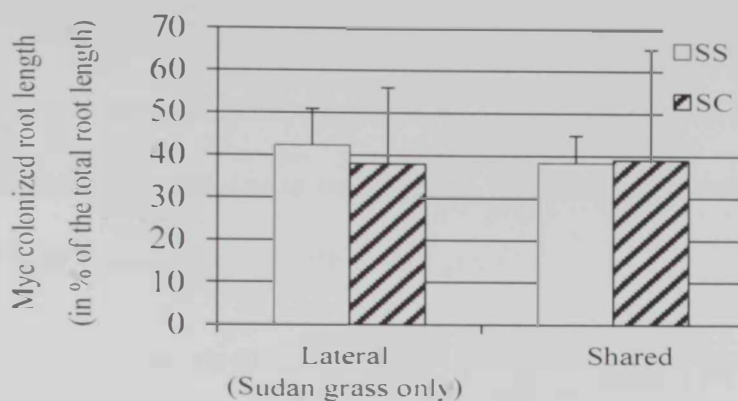


Figure 24: The endomycorrhiza colonized root length in percent of the total root length. The values are means obtained for mycorrhiza inoculated plants of the SS and the SC treatments. Of the lateral roots of the SC treatment, only values obtained for Sudan grass plants are shown. *Cyperus conglomeratus* roots grown in absence of Sudan grass roots were found to be nonmycorrhizal. In shared compartments no distinction between Sudan grass and *C. conglomeratus* roots could be made. A One Way ANOVA (Tukey's multiple comparison) did not reveal significant ( $P < 0.005$ ) differences between the mean values that are shown.

### 2.3.3 Element analysis

The concentrations of P in shoots of *C. conglomeratus* and Sudan grass plants were in a similar range when the soil was not inoculated with mycorrhizal fungi. Mycorrhiza inoculation increased shoot concentrations of P in Sudan grass, but there was no effect of mycorrhiza on P concentrations in *C. conglomeratus* shoots. (Tables 8, 9 and 10).

Concentrations of K and Na were higher in shoots of *C. conglomeratus* compared with Sudan grass plants. The Na concentrations in *C. conglomeratus* shoots increased in response to mycorrhizal inoculation, while the K concentration decreased. When *C. conglomeratus* grew together with Sudan grass, Na concentrations in the shoot were lower compared with *C. conglomeratus* plants that shared the central compartment with another plant of the same species.

Concentrations of Mg and Ca were similar between *C. conglomeratus* and Sudan grass. There was no effect of mycorrhiza inoculation or the identity of the neighboring plant on shoot Mg concentrations. Ca concentrations were increased in *C. conglomeratus* shoots in response to mycorrhizal inoculation, particularly when the plants shared middle compartment with Sudan grass.

Micronutrient concentrations were generally higher in *C. conglomeratus* compared with Sudan grass shoots. Mycorrhiza inoculation decreased concentrations of Fe in the shoots of Sudan grass plants, but there was no other effect of the experimental treatments on the micronutrient concentrations in the shoots of *C. conglomeratus* and Sudan grass.

Table 8: Element concentrations in shoot material obtained from Sudan grass and *C. conglomeratus* plants in mg per g DW for macronutrients, and in  $\mu\text{g}$  per g DW for micronutrients.

		S		C	
		SS	SC	CC	SC
P (mg per g DW)	Non-Myc	0.56	0.50	0.58	0.50
		$\pm 0.23$	$\pm 0.11$	$\pm 0.07$	$\pm 0.15$
	Myc	0.66	1.17	0.74	0.67
		$\pm 0.25$	$\pm 0.43$	$\pm 0.12$	$\pm 0.33$
K (mg per g DW)	Non-Myc	10.16	10.01	15.90	15.20
		$\pm 1.03$	$\pm 1.34$	$\pm 1.68$	$\pm 1.96$
	Myc	8.99	10.11	14.09	13.56
		$\pm 2.16$	$\pm 4.51$	$\pm 0.60$	$\pm 1.20$
Mg (mg per g DW)	Non-Myc	2.38	2.21	2.06	1.89
		$\pm 0.12$	$\pm 0.13$	$\pm 0.14$	$\pm 0.07$
	Myc	2.17	2.30	2.08	2.20
		$\pm 0.21$	$\pm 0.40$	$\pm 0.34$	$\pm 0.22$
Ca (mg per g DW)	Non-Myc	5.35	4.92	5.61	4.49
		$\pm 0.99$	$\pm 0.57$	$\pm 0.84$	$\pm 0.26$
	Myc	5.06	5.07	6.21	6.41
		$\pm 0.57$	$\pm 1.75$	$\pm 1.18$	$\pm 1.15$
Na (mg per g DW)	Non-Myc	0.44	0.31	2.31	1.57
		$\pm 0.25$	$\pm 0.06$	$\pm 0.40$	$\pm 0.18$
	Myc	0.61	0.33	2.61	2.34
		$\pm 0.55$	$\pm 0.30$	$\pm 0.20$	$\pm 0.40$
Fe ( $\mu\text{g}$ per g DW)	Non-Myc	99.39	97.36	241.13	198.99
		$\pm 9.37$	$\pm 13.01$	$\pm 64.67$	$\pm 43.19$
	Myc	85.41	77.00	243.44	277.28
		$\pm 10.68$	$\pm 8.93$	$\pm 69.44$	$\pm 121.27$

		S		C	
		SS	SC	CC	SC
Cu (µg per g DW)	Non-Myc	5.50	5.31	7.62	9.06
		±0.46	±1.13	±0.59	±2.49
	Myc	5.39	7.01	6.67	8.10
		±1.45	±0.50	±0.46	±0.43
Zn (µg per g DW)	Non-Myc	86.33	86.62	148.05	148.14
		±6.63	±21.99	±9.56	±22.39
	Myc	88.42	89.80	111.70	130.34
		±20.05	±20.30	±27.15	±34.50
Mn (µg per g DW)	Non-Myc	19.05	19.10	34.76	30.99
		±3.75	±0.98	±3.14	±4.39
	Myc	19.80	19.67	30.36	29.73
		±3.60	±7.72	±4.18	±4.28

The values are the means ± standard deviations. Shoot material that was lost or cut off throughout the growth period was included into this analysis. For treatment abbreviations see Fig. 18.



Table 9: Results of the Two Way ANOVA performed on data obtained for element concentrations in the shoots of Sudan grass and *C. conglomeratus* plants.

ANOVA								
	S				C			
	Myc		N		Myc		N	
	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value
P	<b>0.024</b>	6.848	0.149	2.413	0.146	2.452	0.469	0.563
K	0.716	0.140	0.740	0.116	<b>0.050</b>	4.847	0.452	0.608
Mg	0.669	0.193	0.850	0.0375	0.146	2.446	0.832	0.0470
Ca	0.900	0.0165	0.720	0.136	<b>0.021</b>	7.177	0.345	0.973
Na	0.605	0.284	0.282	1.281	<b>0.008</b>	10.299	<b>0.012</b>	9.013
Fe	<b>0.011</b>	9.465	0.370	0.875	0.359	0.917	0.923	0.00971
Cu	0.159	2.283	0.205	1.816	0.208	1.787	0.070	4.040
Zn	0.795	0.0707	0.934	0.00711	0.061	4.364	0.485	0.522
Mn	0.794	0.0715	0.987	0.000274	0.203	1.828	0.315	1.109

For treatment abbreviations see Fig. 18. P values indicative of a significant ( $P < 0.05$ ) influence of mycorrhizal inoculation (Myc), or the neighboring species (N) are printed in bold. Two Way ANOVAs did not reveal any significant interactions.

The shoot P content was approximately the same between Sudan grass and *C. conglomeratus* plants when the soil was not inoculated with mycorrhizal fungi (Tables 10, 11 and 12). In response to mycorrhiza inoculation, Sudan grass took up an increasing amount of P into the shoot, while *C. conglomeratus* shoot uptake of P remained unaffected. The shoot P content was unaffected by the identity of the respective neighboring plant in both, *C. conglomeratus* and Sudan grass.

The uptake of K, Mg and Na into Sudan grass shoots was neither affected by mycorrhiza inoculation, nor by the identity of the neighboring plant. Shoot uptake of K was in a similar range for Sudan grass and *C. conglomeratus* plants. Mg uptake was greater for shoots of Sudan grass compared with *C. conglomeratus*, while Na contents were generally higher in *C. conglomeratus*.

The micronutrient contents were approximately the same between Sudan grass and *C. conglomeratus* plants. Mycorrhiza inoculation decreased contents of Cu, Zn and Mn in the shoots of *C. conglomeratus* plants, but there was no other effect of the experimental treatments on micronutrient contents in shoots of *C. conglomeratus* and Sudan grass.

Table 10: Element content of shoots obtained from Sudan grass and *C. conglomeratus* plants in mg per plant for macronutrients, and in µg per plant for micronutrients.

		S		C	
		SS	SC	CC	SC
P (mg per plant)	Non-Myc	2.23	3.02	2.42	2.54
		±0.96	±1.82	±0.66	±1.12
	Myc	4.64	7.93	2.75	1.60
		±1.15	±5.58	±0.93	±1.36
K (mg per plant)	Non-Myc	43.31	55.08	67.40	73.53
		±21.87	±18.29	±15.01	±8.70
	Myc	63.52	46.62	57.04	31.72
		±27.16	±27.80	±23.91	±13.05
Mg (mg per plant)	Non-Myc	9.80	12.44	8.30	9.32
		±3.89	±4.99	±2.50	±2.09
	Myc	15.01	12.58	7.72	4.97
		±3.95	±8.79	±2.76	±1.62
Na (mg per plant)	Non-Myc	1.47	1.66	9.44	7.66
		±0.47	±0.52	±2.81	±1.36
	Myc	2.24	1.07	8.99	5.17
		±0.53	±0.48	±2.74	±1.44
Fe (µg per plant)	Non-Myc	414.37	578.99	862.22	1006.92
		±193.06	±324.30	±212.89	±436.70
	Myc	611.58	477.44	873.06	559.75
		±236.90	±352.48	±391.04	±79.99
Cu (µg per plant)	Non-Myc	21.50	28.62	31.75	44.46
		±7.47	±8.78	±10.21	±13.74
	Myc	35.23	40.12	26.45	18.96
		±8.15	±27.76	±9.61	±8.00
Zn (µg per plant)	Non-Myc	354.98	458.30	615.47	712.90
		±151.94	±100.85	±159.69	±59.78
	Myc	572.82	470.60	439.98	317.75
		±134.57	±283.92	±89.30	±171.75
Mn (µg per plant)	Non-Myc	78.26	107.81	146.31	152.17
		±41.59	±43.66	±36.80	±35.52
	Myc	134.47	95.17	115.87	71.29
		±30.32	±61.17	±33.86	±36.81

The values are the means ± standard deviations. Shoot material that was lost or cut off throughout the growth period was included into this analysis. For treatment abbreviations see Fig. 18.

Table 11: Results of the Two Way ANOVA performed on data obtained for element content in the shoots of Sudan grass plants.

	ANOVA						Interaction Factor
	Myc		N		Interactions		
	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	
P	0.047	4.984	0.239	1.550			
K	0.651	0.216	0.843	0.0411			
Mg	0.402	0.760	0.974	0.00115			
Na	0.749	0.108	0.087	3.520	0.024	6.850	Myc X N
Fe	0.758	0.0998	0.922	0.0101			
Cu	0.160	2.266	0.488	0.514			
Zn	0.255	1.442	0.996	0.0000325			
Mn	0.381	0.832	0.842	0.0417			

For treatment abbreviations see Fig. 18. P values indicative of a significant ( $P < 0.05$ ) influence of mycorrhizal inoculation (Myc), the neighboring species (N), or a significant interaction between both factors are printed in bold. Two Way ANOVAs did not reveal any significant interactions.

Table 12: Results of the Two Way ANOVA performed on data obtained for element content in the shoots of *C. conglomeratus* plants.

	ANOVA			
	Myc		N	
	P-Value	F-Value	P-Value	F-Value
P	0.594	0.302	0.375	0.855
K	<b>0.007</b>	10.807	0.252	1.463
Mg	0.058	4.493	0.473	0.551
Na	0.215	1.735	<b>0.029</b>	6.309
Fe	0.199	1.871	0.608	0.279
Cu	<b>0.018</b>	7.667	0.648	0.220
Zn	<b>0.002</b>	17.251	0.860	0.0326
Mn	<b>0.013</b>	8.857	0.323	1.072

For treatment abbreviations see Fig. 18. P values indicative of a significant ( $P < 0.05$ ) influence of mycorrhizal inoculation (Myc), or the neighboring species (N) are printed in bold. Two Way ANOVAs did not reveal any significant interactions.

## 2.4 Discussion

### 2.4.1 Effect of mycorrhiza inoculation on P uptake and growth of Sudan grass and *C. conglomeratus* grown with roots sharing the same soil volume

In the present experiment, P was supplied only to the central root compartment, which was shared between either plants of the same, or different species. In all plants of this study, the shoot concentrations of P at the time of harvest were indicative of severe deficiency. This suggests that P availability may have been a limiting factor for plant performance.

It was hypothesized that Sudan grass, which is a mycotrophic plant, and *C. conglomeratus*, which is a non-host to mycorrhizal fungi, would exploit different pools of soil P, and thus compete only little for uptake of this element from a shared rooting zone. To some extent the results of the present experiment confirm this hypothesis. Mycorrhiza inoculation increased P uptake in Sudan grass. However, inoculated Sudan grass plants that shared the middle compartment with *C. conglomeratus* did not take up more P compared with plants that grew together with another plant of the same species. In *C. conglomeratus*, neither shoot P concentrations nor contents were affected by the identity of the neighboring plant species, irrespective of mycorrhiza inoculation. This suggests that neither *C. conglomeratus* nor Sudan grass outcompeted a neighbor of the respective other species in terms of shoot P uptake.

On the other hand, sharing the central compartment with a Sudan grass plant instead of another *C. conglomeratus*, reduced shoot and root growth of the desert sedge. Root concentrations and contents of P were not analyzed, and thus it can not be excluded that total plant P uptake was higher for Sudan grass compared with *C.*



*conglomeratus*. Since the negative effect of the presence of Sudan grass roots on the growth of *C. conglomeratus* was particularly pronounced in mycorrhiza inoculated treatments, it can also not be excluded that direct negative effects of the presence of living mycorrhizal fungi on the non-host played a role.

Mycorrhizal fungi are known to assist plants in nutrient uptake. The arbuscular mycorrhizal plant can help the mycorrhizal plant to acquire nutrients by extending the hyphae more than 10 cm (Li et al., 1991a; Jakobsen et al., 1992) and hyphal densities >10 meters of hyphae per gram of soil (Jakobsen et al., 1992; Drew, et al., 2003; Cavagnaro et al., 2005). In this study mycorrhizal Sudan grass plants had much higher contents of P in their shoots compared with the corresponding Non-Myc controls. A contribution of mycorrhiza fungal root colonization to uptake of P has been reported by numerous authors e.g. Gianinazzi-Pearson and Gianinazzi (1983), Pearson and Jakobsen (1993), Smith et al. (2003), Poulsen et al. (2005), Landis et al. (2005), Reynolds et al. (2005), Smith and Read (2008), Wang et al. (2010), Smith and Smith, (2011b) and Ortas et al. (2011). Cavagnaro et al. (2015) showed that the arbuscular mycorrhizal fungi can provide their host plant with up to 90 % of plant P, but that percentage varied across studies. Though a contribution to net plant P uptake is one of the most commonly reported effects of mycorrhiza fungal root colonization, there are also reports where the presence of mycorrhizal fungi had no or even a negative effect on growth or nutrient uptake of host plants. For example, Andrade et al. (2010) showed that the arbuscular mycorrhizal fungi did not change the nutrition of host plants, and was of no advantage compared with the non-mycorrhizal status. Such differences in the outcomes of mycorrhiza studies may be explained by different experimental conditions, as well as different plant and fungal species involved. Koehl and van der

Heijden (2016) found that different arbuscular mycorrhizal fungi taxa had different effect on plant P uptake.

The net contribution of arbuscular mycorrhizal fungi to P uptake of their host plants has often been shown to depend on the soil P availability. With a low P availability, the yields of plants were found to be highly dependent on their mycorrhizal status under greenhouse conditions (Ortas, 2003). Cavagnaro et al. (2015) suggested that the highest arbuscular mycorrhizal benefits in terms of plant growth and nutrition were found under P limiting conditions. Under these conditions, the mycorrhiza fungal contribution to plant P uptake is of particular advantage (Sharif and Claassen, 2011).

Compared with standard values cited by Bergmann (1992), the P concentrations in shoots of Sudan grass and *C. conglomeratus* were indicative of severe P deficiency. Though mycorrhiza inoculation increased total plant P uptake of Sudan grass plants in the present study, the mycorrhiza symbiosis did not restore a sufficient P supply range as reported in some previous studies (Neumann et al., 2009).

It is believed that arbuscular mycorrhizal fungi support plant P acquisition mainly by increasing its spatial plant availability. The additional nutrient absorbing surface provided by the arbuscular mycorrhizal fungi can be far larger than that provided by root hairs alone (Sanders and Tinker, 1973). In the arbuscular mycorrhizal fungi, a network of extraradical hyphae spreads around the root. The extraradical hyphae expand the absorption root area and can pass through the root P depletion zone (Li et al., 1991a). It has been shown that mycorrhiza fungal hyphae can reach to distances of up to 15 cm away from the root surface (Jakobsen et al., 1992). The extraradical hyphae transports P into the intraradical hyphae, and into the arbuscules.

The latter are believed to constitute the apoplastic interface for exchange of nutrients between the plant and fungus (Parniske, 2008; Smith and Read, 2008).

In the present study, shoot P uptake did not differ much between the treatments when the soil was not inoculated with mycorrhizal fungi. On inoculated soil, however, Sudan grass took up more than twice as much P as on noninoculated substrate. Despite this strong increase in P acquisition of the neighbor, SC *C. conglomeratus* shoot P contents did not significantly decrease compared with the noninoculated controls. This may suggest that P pools available to mycorrhizal fungi and *C. conglomeratus* roots were not entirely the same. It could be speculated that *C. conglomeratus* chemically increases P availability, while mycorrhizal fungi spatially increase P availability. This clearly needs further investigation, but the high Fe concentrations in the *C. conglomeratus* tissues may be a hint that *C. conglomeratus* mobilized P chemically (which often also results in an increase in Fe availability).

Some plant species which are non-hosts to arbuscular mycorrhizal fungi have evolved strategies for chemical nutrient mobilization, such as cluster roots (Shane et al., 2006). Though mycorrhizal fungi have been shown to acidify the hyphosphere (Wang et al., 2013), and to actively mobilize nutrients (Ortas, 2012) in some studies, it may be energetically of advantage for plants to release organic acids directly via the root surface, and not via the fungal symbiont. Some studies suggest that roots of rhizosheath forming plant species assume a similar function as cluster roots (Abrahão et al., 2014). Thus, it could be speculated that in the present study, *C. conglomeratus* chemically mobilized P, while mycorrhiza fungal inoculation made P available spatially. Phosphate mobilization via rhizosphere, pH decrease and release of organic

acids can be of particular advantage on P fixing soils, such as sodic or acid soils (Abrahão et al., 2014).

Previous studies have shown that the arbuscular mycorrhiza fungal root colonization can increase the competitive strength of host plants against non-mycorrhizal weeds in terms of P uptake and above and belowground biomass (Weisany et al., 2016). The nonmycorrhizal status can be of disadvantage compared with the mycorrhizal situation not only in terms of competition for soil nutrient resources, but possibly also because of active antagonism between arbuscular mycorrhizal fungi and non-hosts. A release of allelopathic compounds by mycorrhiza fungal hyphae, which lead to decrease root development and thus poorer nutrient uptake in non-hosts has been postulated by some authors (Francis and Read, 1994, 1995). Some other studies, however, confirm the observation that the ability of a non-host to acquire P does not change when mycorrhizal roots share the same soil volume (Daisog et al., 2012).

Even though the identity of the neighboring plant had no effect on the shoot P content, there may have been an effect on the total plant N uptake (which could not be analyzed). The shoot and root dry weight of the *C. conglomeratus* plants was negatively affected by a neighboring mycorrhizal Sudan grass, and it can not be completely ruled out that a reduction in total N uptake was responsible for this. There was no effect of the identity of the neighboring plant species on the shoot uptake of P and K, suggesting that competition for other macronutrients may not have played a major role, as intended by the experimental set-up. However, N concentrations in the tissues were not analyzed, and it can thus not be ruled out that Sudan grass had a better ability to acquire N from the shared root compartment compared with *C.*

*conglomeratus* when the soil was mycorrhiza inoculated. A contribution of the arbuscular mycorrhiza fungal symbiosis to plant N uptake has frequently been observed.

The dry weight of the roots obtained from the outer pots in the present experiment was higher for nonmycorrhizal compared to mycorrhizal *C.conglomeratus* when grown together with Sudan grass. *Cyperus conglomeratus* is a non-host to mycorrhizal fungi. Several previous studies have reported that the presence of actively growing mycelia of arbuscular mycorrhizal fungi can affect nutrient uptake and growth of these plants. For example, Neumann and George, (2005) and Smith et al. (2009) showed that the presence of arbuscular mycorrhiza mycelia can reduce P uptake of non-host plants. Veiga et al. (2013) found that mycelial networks of arbuscular mycorrhizal fungi sustained by an actively growing host plant infected the roots of neighboring non-host species *Arabidopsis thaliana*, and caused 50 % biomass reduction in the latter. The mechanisms by which non-host plants are negatively affected by the presence of mycorrhiza mycelia of the neighboring host plants, is not yet completely understood. In some cases, non-host plants showed incomplete intraradical mycorrhiza colonization (Daisog et al., 2012). Mycorrhiza fungal structures on the surface or within the cortex were, however, not observed in any of the *C. conglomeratus* roots. Puschel et al. (2007) showed that mycorrhiza fungal root colonization of non-host plants required a pre-existing extraradical mycelial networks, and could not be established from resting spores in the soil.

Though mycorrhiza colonization of *C. conglomeratus* roots was not observed in the present study, it can not be excluded that the hyphae sustained by neighboring Sudan grass root systems attempted to colonize the roots of the sedge. This may have



initiated defense responses against the approaching fungal mycelium in the non-host, which may have had a negative impact on growth. Facelli et al. (2010) reported that arbuscular mycorrhiza fungal hyphae sustained by an actively growing host plant repeatedly attempted to infect neighboring non-host roots. The fungi formed hyphae near the surface of the non-host roots, and formed hyphal coils in their cortical cells. In response to these colonization attempts, the growth of the non-host was decreased. Negative effects of arbuscular mycorrhizal mycelia on neighboring non-host plants have also been reported by Francis and Read (1995). In line with these findings, Malcova et al. (2001), Sykorova et al. (2003) and Enkhtuya et al. (2005) found that extraradical mycelial networks connected to host roots (maize or *Solanum nigrum*) played an important role in infecting the root systems of neighboring *Chenopodium album* plants (non-host). According to Francis and Read (1994 and 1995) arbuscular mycorrhizal fungi colonizing sunflowers (hosts), produced toxic compounds which caused negative effects on non-host weeds.

Though the extent of arbuscular mycorrhiza fungal root colonization was not low in the present experiment in inoculated Sudan grass roots, there was no difference in dry weight between mycorrhiza inoculated and non-inoculated Sudan grass shoots. Despite a significant contribution of mycorrhiza inoculation to shoot P uptake, it seems there was no benefit in terms of plant dry weight production. Mycorrhiza inoculation had no influence on the dry weight or growth of the Sudan grass roots in the single pots.

Several authors have suggested that plant species differ in their responsiveness to arbuscular mycorrhiza fungal root colonization when grown in planting pots under controlled conditions (Watkinson and Freckleton, 1997). Wagg et al. (2011). Bender

et al. (2014) and Köhl et al. (2014) reported that *Lolium multiflorum*, like many grasses, is colonized by arbuscular mycorrhizal, but no strong response in terms of dry weight gain can be observed when mycorrhizal and nonmycorrhizal controls are compared. Other authors also observed that the mycorrhiza benefits in terms of growth response depend on the host species (Siqueira et al., 1998; Kiers et al., 2000; Zangaro et al., 2000, 2003).

Smith and Smith (2011a) showed that arbuscular mycorrhiza fungal root colonization enhances growth of tomato under some conditions, but the same host species can be non-responsive to the colonization as well. In return for their contribution to plant nutrient acquisition, the symbiotic soil fungi are supplied by the plant with carbohydrates in form of hexose (Cavagnaro et al., 2010; Feddermann et al., 2010; Hart and Forsythe, 2012; Xie et al., 2014). The trade of nutritional elements for photoassimilates between plants and fungi, however, does not always seem to result in mutual benefits. According to Hart and Reader (2002), carbon can be sent to the arbuscular mycorrhizal fungi from plants that do not at the same time benefit from fungal contributions to plant nutrition. Also, Johnson et al. (1997) found that if the carbon demand of arbuscular mycorrhizal fungi is more than mycorrhizal benefits to plants, this can cause negative effects on plant growth. The outcome of the mycorrhiza fungal symbiosis for the plant may depend on the functional compatibility between host and fungal partner. Though endomycorrhizal fungi are rather non-specific in terms of symbiosis establishment, the functionality of the association in terms of nutrient exchange may differ in a wide range. Ravnskov and Jakobsen (1995), Avio et al. (2006) and Scheublin et al. (2007) reported that different plant species respond in a different way to different arbuscular mycorrhizal fungi. Köhl and van der Heijden (2016) found that the different arbuscular mycorrhiza fungal taxa differentially



influenced plant performance. In accordance, Klironomos, (2003) showed that some arbuscular mycorrhizal taxa decreased the growth of one plant species, but encouraged the growth of another grown under the same conditions. In natural habitats, mycotrophic plants have been shown to exhibit a preference for certain arbuscular mycorrhiza fungal strains. The outcome of the mycorrhizal symbiosis to plant performance and competitive strength may depend on whether a plant finds a functionally compatible arbuscular mycorrhiza fungal strain, or not (van der Heijden et al., 1998; Feddermann et al., 2010). In the present experiment, plants were inoculated with rhizosphere soil obtained from an agricultural field. It can be assumed that more than one arbuscular mycorrhiza fungal species was present in this inoculum, and that this would have increased the chances for Sudan grass to find a functionally compatible fungal partner. The observation that P uptake but not growth was increased in Sudan grass in response to mycorrhiza fungal inoculation, suggests that the association was functionally compatible. Whether carbon expenditure for the mycorrhizal symbiosis limited the ability of mycorrhizal plants of the present study to grow, remains speculative. It is also possible that another factor, e.g. N nutrition, limited plant growth. In accordance with our results, Daisog et al. (2012) reported that maize biomass was not increased by mycorrhization. However, the plants benefitted from arbuscular mycorrhizal fungi via enhanced P uptake. In other plant species, arbuscular mycorrhiza fungal contributions to P uptake which are not translated into better growth have also been observed (Landis et al., 2005; Reynolds et al., 2005; Smith and Read, 2008; Smith and Smith, 2011b). Such effects may depend on the plant and fungal partners involved (Douds and Reider, 2003), but also on the growing conditions (Bryla and Koide, 1990; Jakobsen et al., 1992). Fitter (1991) showed that

the high carbon drain by the fungal symbionts can cause the absence of mycorrhiza benefits in terms of plant growth.

The nonmycorrhizal plants were also colonized by mycorrhizal fungi. It can not be excluded that differences between mycorrhizal and nonmycorrhizal Sudan grass plants in terms of growth and P uptake had been larger if completely nonmycorrhizal controls had been established.

#### **2.4.2 Supply of plants with nutritional elements other than P**

Compared with standard values cited by Bergmann, (1992), concentrations of K in the shoot tissues of plants of all treatments were in a rather low range, and indicative of K deficiency. It is thus likely that K supply was a plant growth limiting factor. *Cyperus conglomeratus* had higher shoot tissue K concentrations compared with Sudan grass when the plants were non-inoculated with mycorrhizal fungi. The presence of mycorrhiza inoculum decreased shoot K concentrations and total shoot K uptake in *C. conglomeratus*, while there was not any effect of mycorrhiza inoculation observed on the K uptake of the Sudan grass shoots. This observation may support the above mentioned idea that there was a direct negative effect of the presence of mycorrhiza functioning on the growth and/or functioning of roots of *C. conglomeratus*. The reasons why *C. conglomeratus* was more successful in shoot K uptake compared with Sudan grass on noninoculated soil remain speculative. It can not be excluded that rhizosheath formation facilitated uptake of nutritional elements (Wei et al., 2011).

Comparing the element concentration of Na in the shoot with maximum threshold limits of Na cited by Kirkby (1992) or Bergmann (1992), it can be concluded that Sudan grass plants of the present experiment were not affected by Na toxicity.

Sodium is sometimes taken up into the plant by the same uptake system as K. Selectivity for K depends on the plant species and the level of affinity of the transporters. Similar with K, the Na concentrations were higher in the shoots of *C. conglomeratus* compared with those in Sudan grass. While mycorrhiza inoculation decreased shoot K concentrations, shoot Na concentrations increased. The K:Na ratio in mycorrhiza inoculated *C. conglomeratus* was in a range between 5.4 and 5.8, which may be slightly below the levels recommended for plants that are rather sensitive to sodicity. The shoot Na concentrations and contents were lower in the *C. conglomeratus* plants when these grew with Sudan grass instead of another plant of the same species. This effect was irrespective of mycorrhiza inoculation. The reasons for this remain speculative. Since *C. conglomeratus* shoots took up more K compared with Sudan grass, it could be that when two desert sedges shared the middle compartment, soil K pools were highly depleted towards the end of the growth period. To satisfy the demand for monovalent cations, *C. conglomeratus* may have taken up relatively more Na under these conditions.

In the present study, Sudan grass and *C. conglomeratus* showed sufficient supply of Mg and Ca in their shoots. Mg contents were lower in the shoots of *C. conglomeratus* compared to those in Sudan grass for both mycorrhizal and nonmycorrhizal plants. An adequate Mg supply level is very important to sustain high concentrations of chlorophyll, which is important for plant photosynthesis (Giri et al., 2003).

Similar with the shoot K/Na ratio, the Ca/Na ratio was lower for *C. conglomeratus* compared with those for Sudan grass, and near the limit below which Na induced Ca deficiency could be expected. When two Sudan grass plants shared the

middle compartment, the shoot K/Na as well as Ca/Na ratios decreased in response to mycorrhiza inoculation. The reasons for this are not known. Such result does not support earlier findings reporting that mycorrhizal fungi protected their host plants from adverse effects of soil salinity (Giri et al., 2007). However, the soil in the present study was not saline, and thus such results may not be easily compared.

Weisany et al. (2016) reported that development of extrametrical hyphae in soil, hyphal absorption of phosphate, translocation of P through hyphae over considerable distances, transfer of P from the fungus to the root cells, plant development stages were important for Mycorrhizal modification of the nutrient uptake properties of roots.

Comparing the element concentrations in the shoot with optimum values cited by (Loop, 1983; Bergmann, 1992) for *Sorghum vulgare*, it can be concluded that, tissue concentrations of P in Sudan grass and *C. conglomeratus* shoots and Mn in sudan grass shoots of mycorrhizal and nonmycorrhizal plants were indicative of deficiency.

Arbuscular mycorrhizal fungi can assist the plant uptake of Cu (Li et al., 1991b; Marschner and Dell, 1994; Toler et al., 2005), Zn (Kothari et al., 1991) and Fe (Clark and Zeto, 2000; Kim et al., 2009).

In the present study the mycorrhizal soil inoculation had no effect on Fe concentrations of *C. conglomeratus* as well as the neighbour had no effect on Fe concentrations in both plant species. In the present experiment mycorrhizal inoculation reduced Fe concentrations in shoots of Sudan grass plants, most likely due to a dilution effect. Fe concentrations were relatively high in all plants of this experiment, but not in a toxic range.

In the present experiment, all the Sudan grass and *C. conglomeratus* plants showed enough and good supply of Cu and Zn concentrations in their shoots. *Cyperus conglomeratus* was also sufficiently supplied with Mn.

Several studies showed that the arbuscular mycorrhizal fungi had a positive effect on Zn uptake and the extensive mycelia could be used for providing Zn (Lehmann et al., 2014). Cavagnaro et al. (2010) reported that the arbuscular mycorrhizal fungi can increase plant Zn uptake under the low soil Zn. Under the high soil Zn, the arbuscular mycorrhizal can protect the plant from Zn accumulation and toxicity. In the current experiment, the presence of mycorrhiza inoculum decreased shoot Zn contents in *C. conglomeratus*, while there was not effect of mycorrhiza inoculation on the Zn uptake of the Sudan grass shoots.

In the present experiment, higher shoot concentrations of Fe and Mn were found in *C. conglomeratus* compared with those in Sudan grass. The differences in micronutrient profiles between the plants could also point to differences in nutrient uptake strategy.



### **Chapter 3: The effect of clipping on the contribution of arbuscular mycorrhizal fungi to salinity tolerance in the groundcover Sudan grass (*Sorghum x drummondii*)**

#### **3.1 Introduction**

Groundwater is the main source of irrigation water for most farmers in the UAE. On more than 80 % of all private farms in the Country, the irrigation water used for the production of forages is brackish. Accumulation of salts in the rooting zone is thus very common in agricultural systems of the UAE, and may have a significant impact on the agricultural productivity.

Sudan grass is commonly grown on soils irrigated with brackish water. It is classified as a moderately salt tolerant by some sources (Begdullayeva et al., 2007), and highly tolerant by others (Sanchez et al., 2002). Though these plants may be unable to exploit their full yield potential when grown on a saline soil, they may still produce reasonable biomass for use as animal fodder.

Association with arbuscular mycorrhizal fungi has been shown to improve the performance of crop plants exposed to root zone salinity (Sannazzaro et al., 2007; Zuccarini and Okurowska, 2008; Khalil et al., 2011; Chandrasekaran et al., 2014; Garg and Pandey, 2015). The precise mechanism behind these effects is not yet completely understood. The mycorrhizal fungi might help the plants to take up nutritional elements from saline soil (Sharifi et al., 2007; Wilson et al., 2012; Garg and Pandey, 2015), or they reduce the transfer of harmful amounts of  $\text{Cl}^-$  and  $\text{Na}^+$  from the root into the shoot (Allen and Cunningham, 1983; Zaccarini and Okurowska, 2008; Estrada et al., 2013b). It is also possible that arbuscular mycorrhizal fungal root colonization facilitates water uptake from soils with a low osmotic potential (Rui'z-



Lozano et al., 1996; Al-Karaki et al., 2001; Cantrell and Linderman, 2001; Porcel et al., 2003; Al-Khaliel, 2010; Hajiboland et al., 2010; Ruiz-Lozano et al., 2012; Fusconi, 2013; Treseder, 2013), or improves the internal water use efficiency (Sheng et al., 2008; Hajiboland et al., 2010; Garg et al., 2014). Formation of mycorrhizas is common among plants native to saline habitats (Evelin et al., 2009), suggesting that at least some strains of arbuscular mycorrhizal fungi may tolerate soil salinity, and support the performance of their host plants under these conditions.

While in some studies no negative effect of soil salinity on the development of the arbuscular mycorrhizal symbiosis could be observed (Wilde et al., 2009; Wu et al., 2010), other authors reported a decline in the extent of arbuscular mycorrhizal fungal root colonization under salt stress (Pfeiffer and Bloss, 1988; van Aarle et al., 2002; Wu et al., 2010; Badda et al., 2014; Krishnamoorthy et al., 2014; Taniguchi et al., 2015). Such effects could be due to inhibited spore germination or growth of the fungal mycelium in a saline medium (Juniper and Abbott, 2006; Porcel et al., 2012). It is also possible that exposure to salinity limits the carbon supply to the fungal symbiont. When exposed to saline soil, additional energy is required by root systems for ion pumping, synthesis of compatible solutes, and maintenance of electrochemical gradients (Rewald et al., 2012). These processes may compete with carbon supply to symbionts. At the same time, the photosynthetic capacity of plants is often reduced in response to salt stress (Mahajan and Tuteja, 2005), potentially leading to a reduced supply of C to the roots. This effect may aggravate in plants that are regularly partially defoliated, such as fodder grasses (Gehring and Whitman, 1994). Clipping off aboveground biomass reduces the overall the photosynthetic capacity of plants (Harley and Smith, 1983; Aguilar-Cham and Guevara, 2016).

Hetrick et al. (1990), Wearn and Gange (2007) and Saravesi et al. (2014) observed a negative effect of clipping on arbuscular mycorrhizal colonization. One of the reasons could be the carbon limitation to the host plants (Medina-Roldán et al., 2008; Barto and Rilling, 2010; Saravesi et al., 2014). Jirout et al. (2009), Garcia et al. (2012) and Saravesi et al. (2014) reported that the most studies on this topic suggest a reduction in arbuscular mycorrhizal root colonization in response to severe defoliation. Nevertheless, there are also studies where arbuscular mycorrhizal colonization remained unaffected by clipping off aboveground biomass (Tian et al., 2009).

The present experiment aimed at investigating the effects of soil salinity and partial defoliation on the relative contribution of the arbuscular mycorrhizal symbiosis to growth and nutrient uptake of Sudan grass. It was hypothesized that arbuscular mycorrhizal fungal root colonization would generally increase plant performance, but this effect would be lower under salinity and in response to clipping. A combination of both, salinity and removal of aboveground biomass would lead to a greater decline in the relative contribution of the arbuscular mycorrhizal symbiosis to plant performance, compared with one of the two factors alone.

## 3.2 Materials and Methods

### 3.2.1 Plant material and seeding preparation

The seeds of Sudan grass were purchased from the local market, and represented a genotype that is commonly grown in the UAE. Sudan grass seeds were germinated on filter paper soaked with a saturated  $\text{CaSO}_4$  solution.

Seedlings of similar size were transferred into cell trays filled with topsoil material from a sand dune in Al Foah, Al Ain, UAE, which was either or not inoculated with arbuscular mycorrhiza fungal propagules. Each cell was filled with 50 cm<sup>3</sup> substrate at a bulk density of 1.6 g per cm<sup>3</sup>. Before it was filled into the cell trays, the soil material was passed through a 1 mm sieve, and was heat sterilized in a drying oven for at least 12 to 20 hours at a temperature of 95 °C. The sterilized soil was fertilized with 150 mg N ( $\text{NH}_4\text{NO}_3$ ), 15 mg P ( $\text{KH}_2\text{PO}_4$ ), 200 mg K ( $\text{K}_2\text{SO}_4$ ), 100 mg Mg ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ), 20 mg Fe (Fe EDTA), 10 mg Zn ( $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ ), 10 mg Cu ( $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ) per kg dry substrate. The inoculum, consisted of a mixture of endomycorrhiza fungal colonised eggplant (*Solanum melongena*) root pieces and adhering air dried soil containing endomycorrhizal hyphae and spores. It was obtained from the Al Foah Experimental Farm near Al Ain, UAE by excavation of fresh root systems of field-grown eggplants in the fruit formation stage. Microscopic observation revealed that more than half of the length of the roots in the inoculum was colonized by arbuscular mycorrhiza fungal structures. The arbuscular mycorrhizal fungal species in the inoculum remained unidentified. The inoculum for the nonmycorrhizal treatments was filtered with deionised water (1000 ml of water through 1500 g of dry inoculum using Double Ring Filter paper Type 102) before being autoclaved. The filtrate was added to the soil to encourage a microflora similar to [mycorrhizal]-

treatments. Each cell of the trays used for raising seedlings was filled with 50 ml of dry, fertilized and inoculated substrate at a bulk density of 1.6 g per cm<sup>3</sup>. To maintain the moisture level in the cells at approximately field capacity, each cell received 5 ml of deionized water daily. One Sudan grass seedling was transferred to each cell, and the plants were cultivated in the trays for 18 weeks before transplanting.

For unknown reasons these plants did not grow after transplanting, and died within six weeks after transfer into larger pots. After the plants had died, their shoots were removed from the planting pots, and new seedlings were raised and transferred to the same planting pots that had been used before.

The second batch of seedlings was established in the same way as the first one. The same substrate, cell trays, and soil sterilization and fertilization procedures were used. After fertilization, 100 ml of viable (mycorrhizal treatments) or autoclaved (nonmycorrhizal treatments) inoculum was incorporated into each kg of dry dune soil. The inoculum was purchased on the local market. According to the German manufacturer's information, it consisted of corn (*Zea mays*) root pieces colonized by the arbuscular mycorrhizal fungus *Rhizophagus irregularis* (formerly '*Glomus intraradices*') and adhering expanded clay carrier material. The inoculum was declared to contain more than 100 infective mycorrhiza fungal propagules per cm<sup>-3</sup> of dry material. The inoculum for the nonmycorrhizal treatments was filtered with deionised water (1000 ml through 800 ml dry inoculum using Double Ring Filter paper Type 102) before being autoclaved. The filtrate was added to the nonmycorrhizal soil to encourage a microflora similar to mycorrhizal treatments. One Sudan grass seedling was transferred to each cell. The plants were grown in the cell trays for 14 weeks before being transplanted to the experimental pots in February 2013. When their roots



were analyzed for mycorrhiza fungal colonization, all samples, including the mycorrhizal treatments, were found nonmycorrhizal.

### **3.2.2 Growth substrate preparation and filling of the experimental pots**

Round plastic planting pots with a total volume of 1.5 L were used in this experiment. Each pot was filled with 1 L of dry sandy dune soil at a bulk density of 1.67 g per cm<sup>3</sup>. The same sandy substrate as for the precultivation in cell trays was used. Planting pots contained 1670 g of sandy soil from the UAEU Experimental Farm in Al Foah and each pot received 150 ml of tap water. Prior to its use in the experiment, the soil had been sieved by passing it through a 1 mm mesh, and then heat sterilized at 95 °C for 12 - 20 hours in a drying oven. The sterilized soil was fertilized in the same way as the soil used for filling the cell trays. The Sudan grass plants were transferred to the experimental pots with the complete root bale comprising all soil of the cell in which they had been precultivated. One plant was transferred into each pot. After transfer, the water content of the soil in the experimental pots was brought to approximately field capacity, and was maintained at this level throughout the growth period. Deionized water was used for irrigation. Any liquid leaching from the bottom of the pots was collected in an underplate and added back to the soil.

### **3.2.3 Establishment of salinity treatments**

Six weeks after transplanting, all Sudan grass plants had rooted in the soil in the experimental pots. By that time, the salinity treatments were established. For this purpose, the soil in the planting pots was either irrigated with brackish or deionized water. Brackish water was established by mixing deionized water with NaCl. Via irrigation with NaCl amended water, the salinity treatments were supplied with in total

3000 mg NaCl per kg dry soil. The first 1500 mg NaCl per kg dry soil was applied 59 days after planting, and another 1500 mg 5 days later. In treatments receiving saline irrigation water, care was taken to apply the same amount of salt to each pot. Control treatments received non-saline irrigation water.

### 3.2.4 Maintenance of the experiment in the greenhouse

The experiment was conducted in a greenhouse (tunnel type, glass fiber cover, open ground, 9 x 36 m) at Al Foah Experimental Farm from February until May 2013. The average greenhouse temperature from February until April was 23 °C during the day, and 18 °C at night. In May the temperature was 30°C during the day, and 26 °C at night). The pots were set up completely randomized (Fig. 25).

The water content in all pots was maintained at approximately 22 % w/w throughout the growth period. Water loss from each pot was estimated gravimetrically and replaced with deionized water.

At 31, 57, 59, 64, 71, 78, 85 and 93 days after transplanting, flowers that some plants had formed were removed to encourage vegetative growth.

The plants of the first batch received additional 100 mg N ( $\text{NH}_4\text{NO}_3$ ), 25 mg P ( $\text{KH}_2\text{PO}_4$ ), 100 mg K ( $\text{K}_2\text{SO}_4$ ), 20 mg Fe (Fe EDTA), 10 mg Zn ( $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ ), 10 mg Cu ( $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ) per kg dry soil which were supplied to the soil. At 29 days after transplanting, the plants of the second batch received additional 100 mg N ( $\text{NH}_4\text{NO}_3$ ), 25 mg P ( $\text{KH}_2\text{PO}_4$ ), 100 mg K ( $\text{K}_2\text{SO}_4$ ), 20 mg Fe (Fe EDTA), 20 mg Zn ( $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ ), 10 mg Cu ( $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ) per kg dry soil. By 57 days after transplanting, 50 mg N ( $\text{NH}_4\text{NO}_3$ ), 25 mg P ( $\text{KH}_2\text{PO}_4$ ), 100 mg K ( $\text{K}_2\text{SO}_4$ ), 100 mg Mg ( $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ) 10 mg Fe (Fe EDTA), 20 mg Zn ( $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ ), 10 mg Cu



( $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ), 15 mg Mn ( $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$ ) per kg dry soil were added. The fertilizer salts were supplied in form of a nutrient solution.



Figure 25: The experiment pots in the greenhouse

### 3.2.5 Defoliation of the plants

Mycorrhizal and nonmycorrhizal plants were either allowed to grow without defoliation (= controls), or were partially defoliated either one or two times throughout the growth period. To partially defoliate the plants, the shoots were cut to a height of 25-30 cm using a scissor. Defoliation was done either only at 64 (1 Cl), or at 64 and 85 days (2 Cl) after transplanting. The pruned material was kept for each plant, and dried at 65 °C in a drying oven.

### 3.2.6 The growth measurements of plants

At 71, 78, 92 and 99 days after transplanting, the shoot lengths, numbers of tillers and numbers of leaves longer than 3 cm were estimated for all plants. The shoot length was measured by a ruler from the soil surface up to the point above which the youngest leaves became visible. In case the plants had tillers, shoot length was

measured for the tallest tiller. The shoot length increment was calculated by subtracting the shoot length at 71 days after transplanting from the shoot length at 78 days after transplanting.

### **3.2.7 Estimation of the endomycorrhiza colonized root length mycorrhiza root colonization**

At 64, 85 and 99 days after transplanting, a soil sample was taken from each planting pot using a cork borer of 1.5 cm diameter and 12 cm length. The roots within the soil core obtained were then washed free from adhering soil, and stained with blue ink using a procedure modified after Vierheilig et al. (1998). For clearing, the root samples were put in a 10 % KOH or NaOH solution for 25 minutes at 65 °C. They were then washed with tap water, put in vinegar for 2 to 3 minutes, then in hot ink solution (50 ml blue ink + 1 L Vinegar) for 5 to 7 minutes. Thereafter, they were kept in tap water with a few drops of vinegar until the endomycorrhiza fungal colonized root length in percent of the total root length was estimated (Tennant, 1975; Kormanik and Mc Graw, 1982).

The extent of arbuscular mycorrhiza fungal root colonization at the time of harvest was assessed through analysis of a root subsample that was taken after roots had been removed from the soil and dried in a drying oven at 65 °C.

### **3.2.8 Harvest and dry weight**

The plants were harvested on the 27<sup>th</sup> of May-2013, at 99 days after transplanting. To harvest the plants, their shoots were cut off above the ground, washed with deionized water, and then dried in paper bags in a drying oven. The substrate with roots was air dried before roots were extracted by passing through a 1 mm sieve.

The dry weight of roots and shoots was estimated after drying of plant material in a drying oven at 65 °C for 24 h.

### **3.2.9 Analysis of the plant material for element concentrations and contents**

For mineral element analysis, the dry plant material was ground into powder using a hammer mill. Samples of 280-310 mg of ground plant material were dry ashed at 550 °C, oxidized with 5 ml of 1:2 diluted HNO<sub>3</sub> and taken up into 25 ml of 1:2 diluted HCl. Concentrations of macro- and microelements in the shoot and root material were measured using ICP-OES.

Root material was not analyzed for micronutrients, as slight soil contamination of the root material could not be excluded. Such contaminations have been shown to affect analyses of iron and possibly other trace metals (Strasser et al., 1999).

Shoot element contents (g per plant) at the time of harvest were calculated by multiplying the element concentrations (g per kg plant material) by the amount of dry weight obtained from the corresponding plants (in kg).

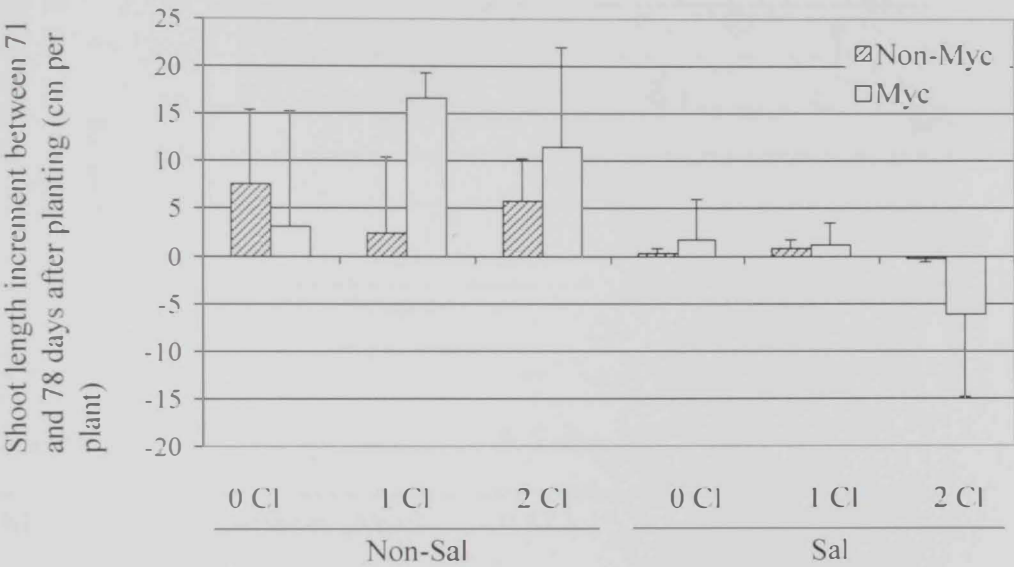
### **3.2.10 Statistical analysis**

Data obtained for treatment replicates was averaged, and the standard deviation was calculated. Data obtained was analyzed by a Three Way ANOVA, testing whether mycorrhizal inoculation, soil salinity or clipping had a significant ( $P < 0.05$ ) effect on the mean values. To test whether individual mean values differed significantly ( $P < 0.05$ ) from each other, Tukey's multiple comparison was performed. Statistical analyses were performed using the SigmaStat 2.03 programme.

3.3 Results

3.3.1 Shoot growth between 71 and 78 days after planting

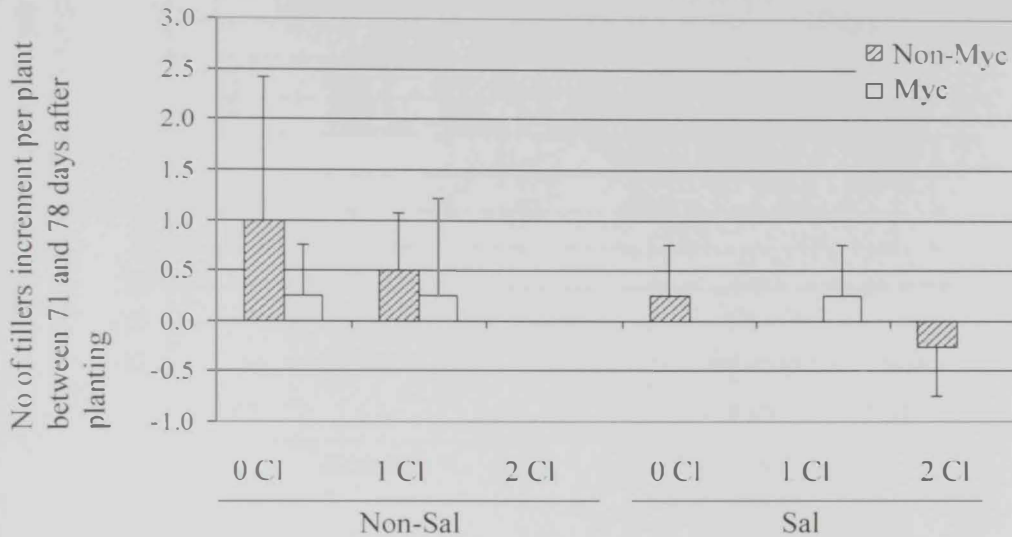
Soil salinity reduced shoot elongation across all mycorrhiza and clipping treatments (Fig. 26). Neither clipping nor mycorrhiza inoculation had an effect on the shoot length growth.



Factor	P-Value
Mycorrhizal inoculation (Myc)	0.324
Saline (Sal)	<b>&lt; 0.001</b>
Clipping (Cl)	0.503

Figure 26: Shoot length increment between 71 and 78 days after planting in cm per plant. The values are the means  $\pm$  standard deviation for plants that were not clipped (0 Cl), clipped one time (1 Cl), or two times (2 Cl), and grown either in saline (Sal) or non-saline (Non-Sal) soil. The table shows the results of the Three Way ANOVA. P-values indicating a significant effect of mycorrhizal root inoculation (Myc), soil salinity (Sal) or plant clipping (Cl) ( $P < 0.05$ ) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line.

There was a high variation in tiller formation between the plants of the same treatment (Fig. 27). Soil salinity and two times clipping tended to reduce tiller formation, but these effects were not significant at  $P < 0.05$ .



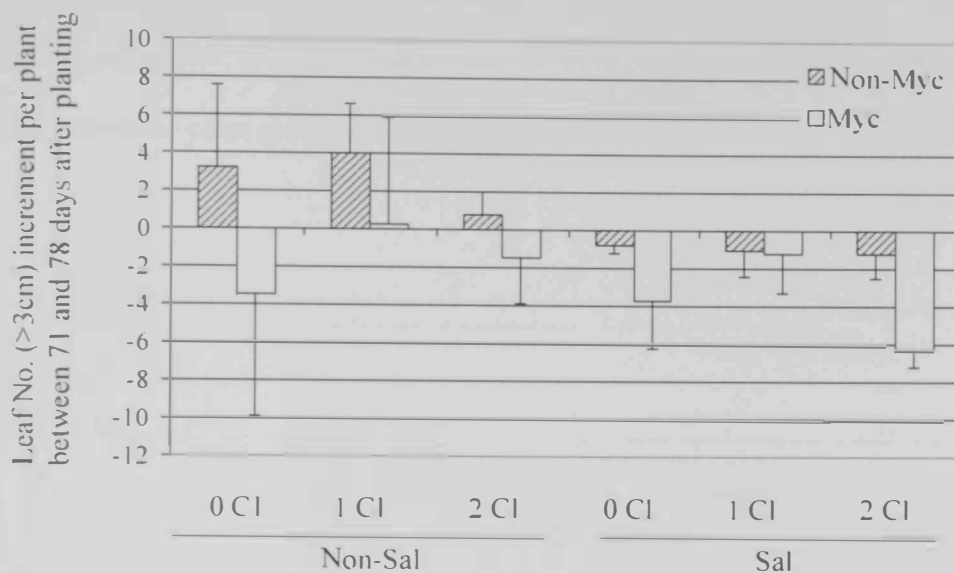
Factor	P-Value
Mycorrhizal inoculation (Myc)	0.472
Saline (Sal)	0.098
Clipping (Cl)	0.115

Figure 27: Number of tillers increment per plant between 71 and 78 days after planting. The values are the means  $\pm$  standard deviation. For treatment abbreviations see Fig. 26. The table shows the results of the Three Way ANOVA. P-values indicating a significant ( $P < 0.05$ ) effect of mycorrhizal root inoculation (Myc), soil salinity (Sal) or plant clipping (Cl) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line.

Soil salinity reduced the formation of leaves with a length greater than 3 cm across all mycorrhiza and clipping treatments (Fig. 28). There was generally a negative effect of mycorrhiza inoculation on the formation of leaves, and this was particularly



pronounced under Saline conditions. Clipping had no effect on the leaf number increment.



Factor	P-Value
Mycorrhizal inoculation (Myc)	<b>&lt; 0.001</b>
Saline (Sal)	<b>0.003</b>
Clipping (Cl)	0.082

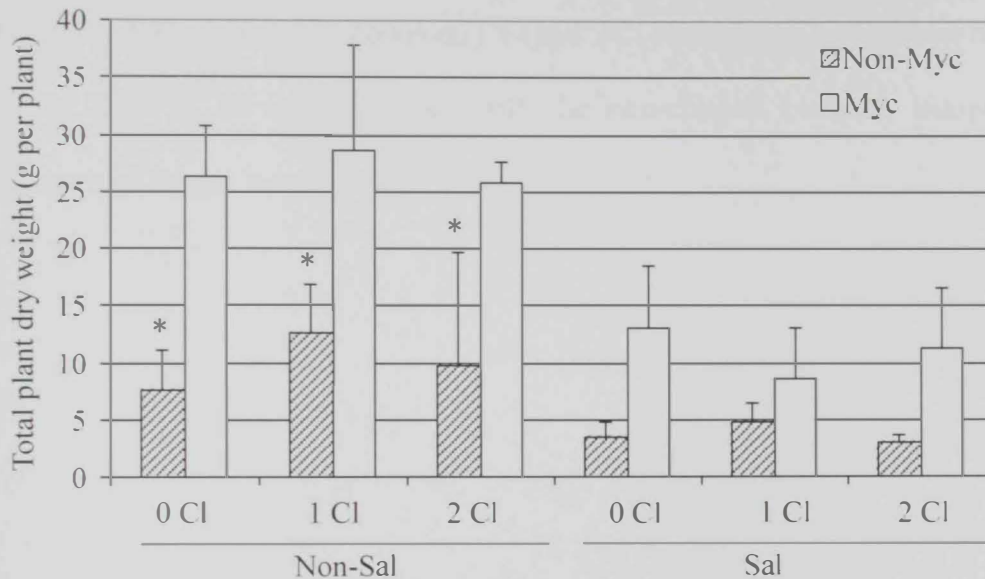
Figure 28: Leaf Number (length >3cm) increment per plant between 71 and 78 days after planting. The values are the means  $\pm$  standard deviation. For treatment abbreviations see Fig. 26. The table shows the results of the Three Way ANOVA. P-values indicating a significant ( $P < 0.05$ ) effect of mycorrhizal root inoculation, soil salinity (Sal) or plant clipping (Cl) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line.

### 3.3.2 Plant dry weight produced throughout the growth period

Soil salinity reduced plant dry weight formed throughout the growth period across all mycorrhiza and clipping treatments (Fig. 29). In all clipping and salinity treatments, mycorrhiza fungal inoculation resulted in an increase in dry weight.



Particularly in the 1 CI treatment, mycorrhiza fungal contribution to plant dry weight production appeared slightly less under saline compared with non-saline conditions. Clipping had no effect on total plant dry weight produced throughout the experiment period, and did also not affect the relative contribution of mycorrhiza fungal inoculation to plant growth.



Factor	P-Value
Mycorrhizal inoculation (Myc)	<b>&lt; 0.001</b>
Saline (Sal)	<b>&lt; 0.001</b>
Clipping (CI)	0.779
Interaction (Myc x Sal)	<b>0.002</b>

Figure 29: Total dry weight produced by the plants throughout the experimental period in g per plant. For treatment abbreviations see Fig. 26. The values are the means  $\pm$  standard deviation. The table shows the results of the Three Way ANOVA. P-values indicating a significant effect of mycorrhizal root inoculation, soil salinity (Sal) or plant clipping (CI) ( $P < 0.05$ ) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. Mean values for nonmycorrhizal plants followed by a star are significantly ( $P < 0.05$ ) different from mean values of corresponding mycorrhizal treatments (Tukey's multiple comparison).

In clipped plants that grew on saline soil, the amount of clipped biomass accounted for a relatively larger proportion of the total shoot biomass compared with corresponding plants that were not exposed to salinity (Fig. 30). In all treatments, salinity increased the proportion of biomass loss throughout the growth period across all mycorrhiza treatments. At the time of harvest, 1 Cl plants that grew on non-saline soil had approximately the same shoot dry weight as the corresponding plants that were not clipped. On saline soil, however, 1 Cl and 2 Cl plants had a lower shoot dry weight at the time of harvest compared with the non-clipped controls, irrespective of mycorrhiza fungal inoculation.

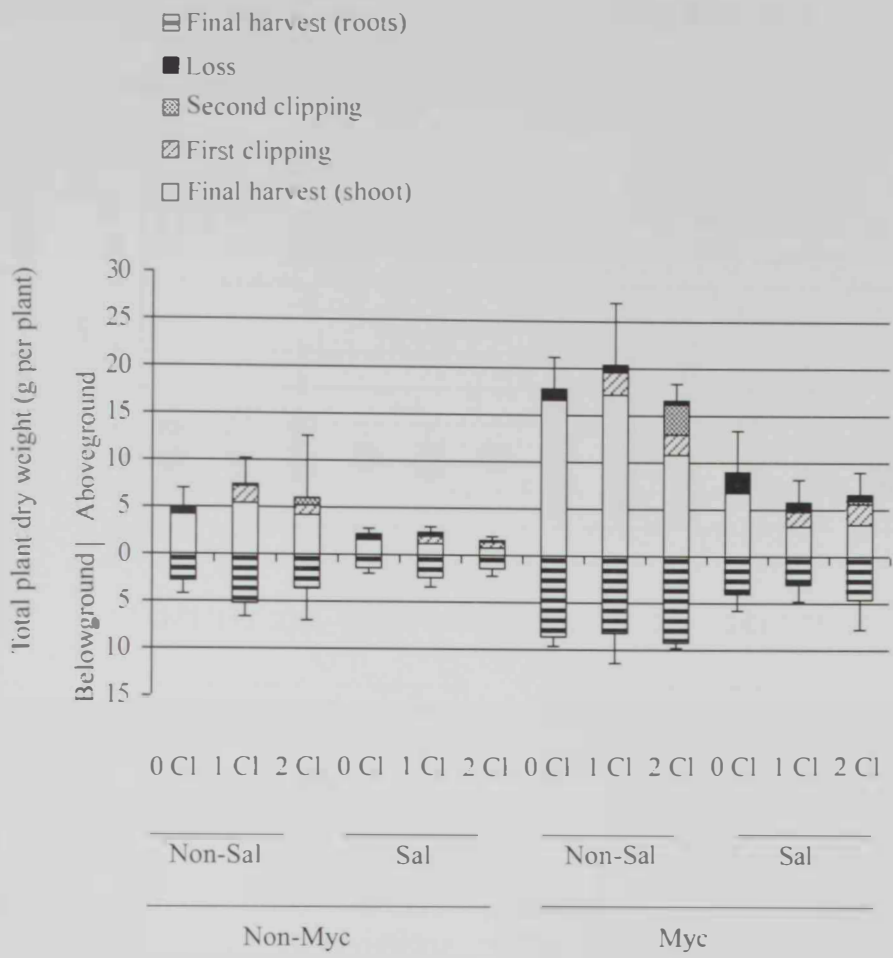


Figure 30: Contribution of different plant fractions to the total plant dry weight in g per plant. For treatment abbreviations see Fig. 26. The values are the means. Standard deviations are shown for the total aboveground and belowground dry weight. Lost biomass (Loss) was collected throughout the whole growth period. 'First clipping' represents dry weight of leaves and flowers pruned 64 DAP, and 'Second clipping' leaf and flower material pruned at 85 DAP. Root dry weight was only estimated at the final harvest.

All plants had formed generative organs by the time of the final harvest (Fig. 31). The generative organs made up approximately the same proportion of total plant dry weight across all treatments. Root inoculation with mycorrhizal fungi increased shoot /root ratio at the final harvest across all clipping and salinity treatments (Fig. 32). Both, exposure to saline soil and clipping reduced the shoot/root ratio. Plants that grew

on saline soil and were clipped one or two times, had the lowest shoot/root ratio among all treatments, irrespective of mycorrhiza inoculation.

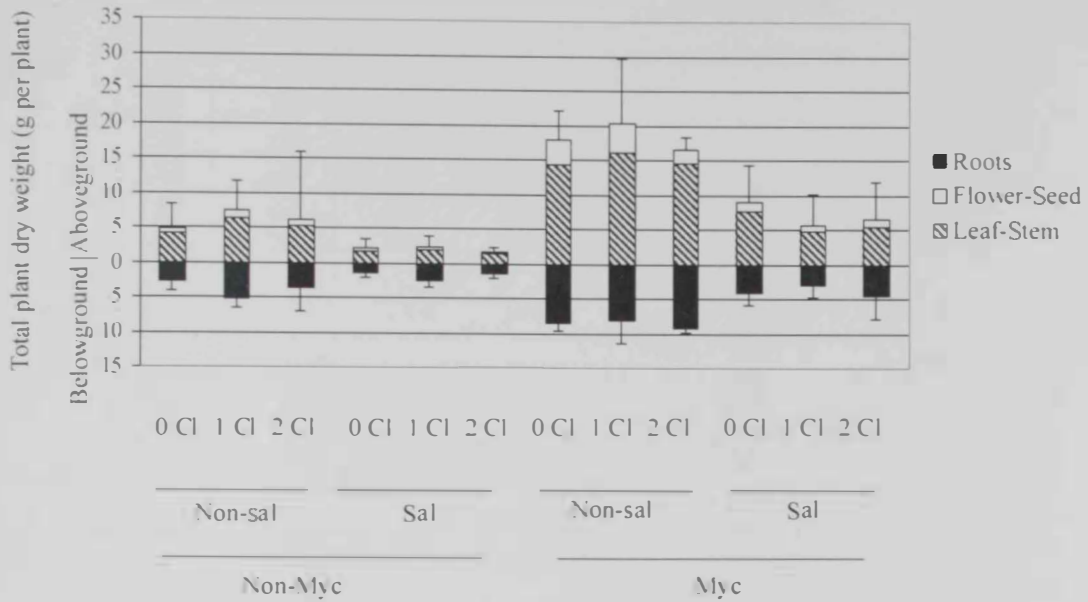
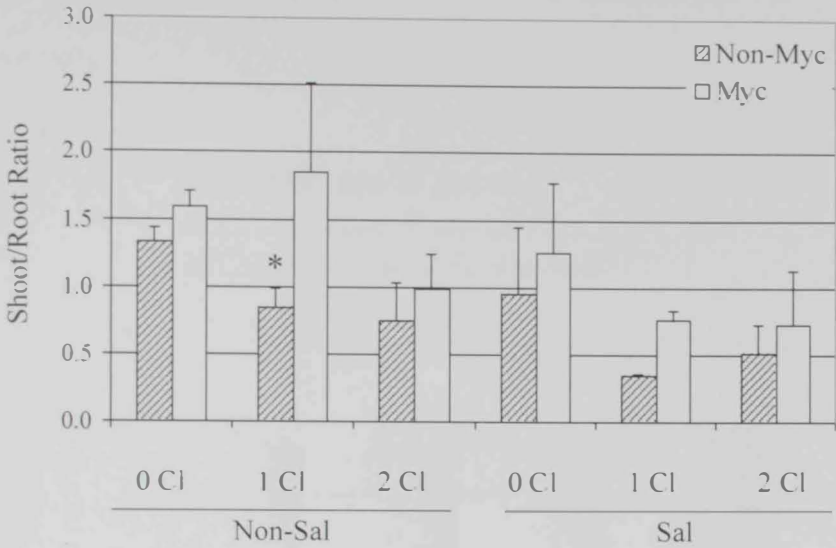


Figure 31: Contribution of different plant parts to the total plant dry weight in g per plant. For treatment abbreviations see Fig. 26. The values are the means. Standard deviations are shown for the total aboveground and belowground biomass. Generative parts (flowers and seeds) and vegetative organs (leaves and stems) were collected throughout the whole growth period. The root dry weight was only estimated at the final harvest.



Factor	P-Value
Mycorrhizal inoculation (Myc)	< 0.001
Saline (Sal)	< 0.001
Clipping (Cl)	< 0.001

Figure 32: Shoot/Root Ratio estimated at the final harvest. The values are the means  $\pm$  standard deviation. For treatment abbreviations see Fig. 26. The table shows the results of the Three Way ANOVA. P-values indicating a significant effect of mycorrhizal root inoculation (Myc), soil salinity (Sal) or plant clipping (Cl) ( $P < 0.05$ ) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line. Mean values for nonmycorrhizal plants followed by a star are significantly ( $P < 0.05$ ) different from mean values of corresponding mycorrhizal treatments (Tukey's multiple comparison).

3.3.3 Arbuscular mycorrhiza fungal root colonization

All plants inoculated with arbuscular mycorrhizal fungi showed colonization rates above 80 % at the time of the final harvest (Figs. 33 and 34). Neither salinity nor the clipping treatment had an effect on the extent of arbuscular mycorrhiza fungal root

colonization. No mycorrhiza root colonization was observed in the non-inoculated controls.

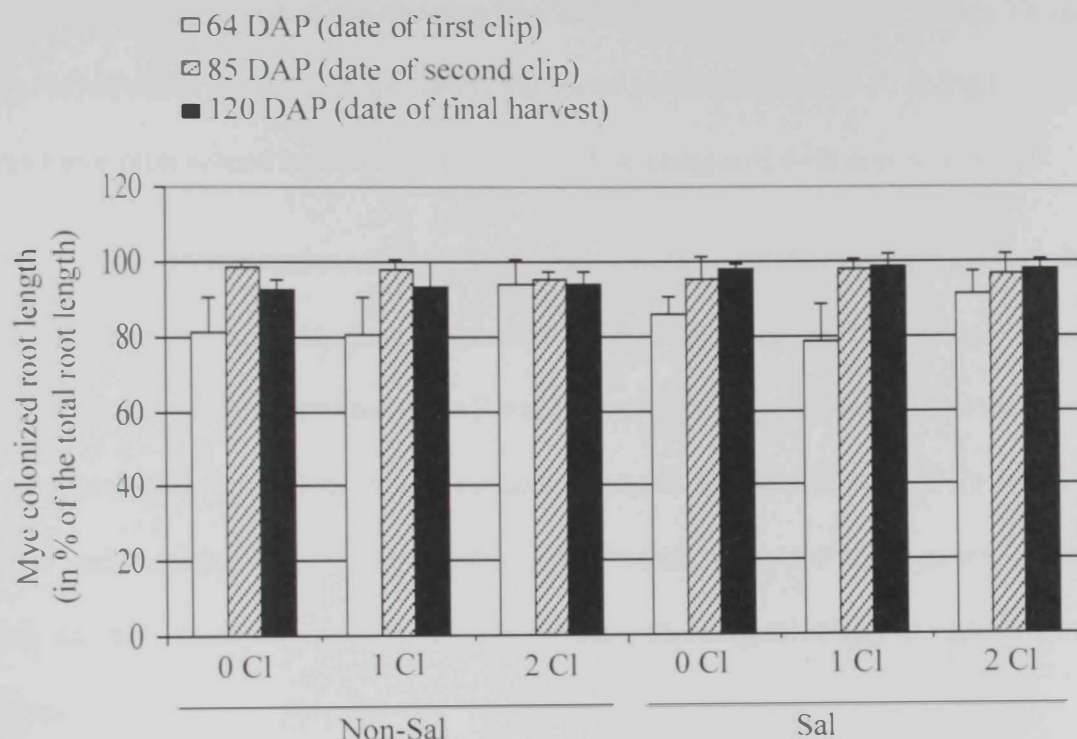


Figure 33: The arbuscular mycorrhiza fungal colonized root length in percent of the total root length. For treatment abbreviations see Fig. 26. The values are the means  $\pm$  standard deviation. The Two Way ANOVA did not reveal a significant ( $P > 0.05$ ) effect of the salinity (Sal) or the clipping (Cl) treatment on the mycorrhiza colonized root length.

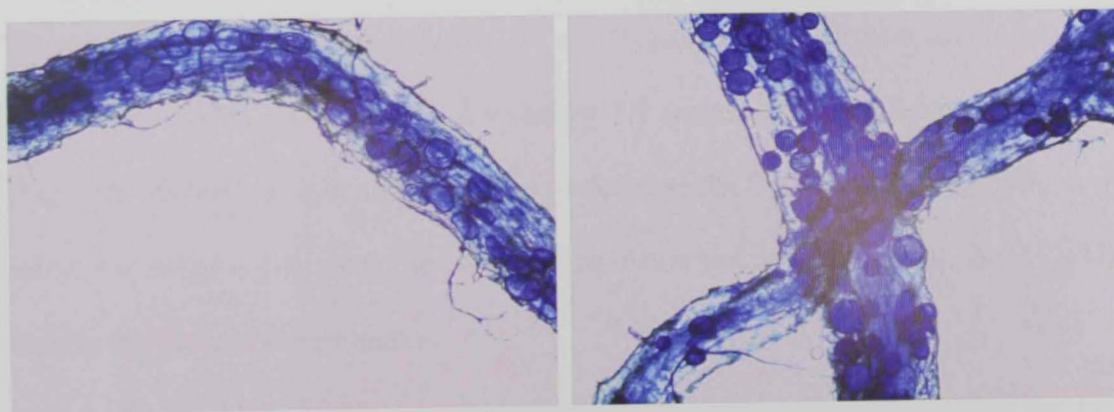


Figure 34: Microscopic images of the fungal colonized roots stained with ink



### 3.3.4 Elements analysis

Clipping plants one or two times within the growth period did not affect the element concentrations in the aboveground biomass that was formed (Tables 13 and 14). Mycorrhiza inoculation increased the shoot concentrations of P, and this effect was more pronounced in plants that grew in saline compared with non-saline soil.

The K concentrations in the shoot tissues were not different depending on the salinity treatment when the plants were nonmycorrhizal. In the mycorrhizal plants, salt application to the soil increased shoot K concentrations compared with plants that grew under non-saline conditions. Shoot concentrations of the divalent cations Ca and Mg decreased in response to Myc inoculation, particularly when the soil was non-saline. Soil salinity increased the Mg and Ca concentrations, particularly in mycorrhizal plants.

There was a strong increase in the Na concentrations in the shoot in response to salt application to the soil. Mycorrhizal plants had higher Na concentrations compared with corresponding non-mycorrhizal controls on saline, but not on non-saline soil.

When plants were grown in non-saline soil the average shoot Ca/Na ratio was between 2.7 and 6.1 (data not shown). In all clipping and mycorrhiza treatments, the Ca/Na ratio of the shoot decreased to below 1.1 in response to soil salt application (Fig. 36). Mycorrhiza inoculation tended to decrease the Ca/Na ratio under both, non-saline and saline conditions. The clipping treatments had no effect on the shoot Ca/Na ratio in the present experiment.

Similar with the Ca/Na ratio, the K/Na ratio severely declined in response to salinity application across all treatments (data not shown). However, neither mycorrhiza inoculation nor clipping had an effect on the K/Na ratio (Fig. 35).

The Fe concentrations in the shoot material showed a relatively high variation across all treatments, resulting in high standard deviations. In shoots of mycorrhizal plants Fe concentrations were lower compared with non-mycorrhizal controls. This effect was particularly pronounced under saline soil conditions.

Mycorrhiza inoculation had no effect on the Cu concentrations, while soil salinity increased Cu concentrations across all mycorrhiza and clipping treatments. Shoot concentrations of Zn and Mn were not affected by any factor tested in this experiment.

Table 13: Element concentrations in shoot material obtained from Sudan grass plants.

		Non-saline soil			Saline soil		
		Not clipped	1 Cl	2 Cl	Not clipped	1 Cl	2 Cl
P (mg per g DW)	Non-Myc	1.13	0.99	1.01	0.77 *	1.17	0.74 *
		±0.41	±0.09	±0.17	±0.04	±0.27	±0.17
	Myc	1.18	1.26	1.25	1.51	1.69	1.65
		±0.11	±0.25	±0.16	±0.47	±0.24	±0.41
K (mg per g DW)	Non-Myc	16.06	14.32	15.44	15.52	13.97	14.16
		±2.68	±1.02	±1.10	±1.21	±1.70	±0.71
	Myc	12.16	13.86	13.98	16.64	16.47	16.11
		±2.25	±2.58	±0.80	±1.21	±0.72	±0.96
Mg (mg per g DW)	Non-Myc	6.28	5.92	6.20	6.63	6.39	7.48
		±2.76	±0.46	±1.16	±0.91	±0.77	±0.39
	Myc	4.42	4.61	5.03	6.67	7.01	6.69
		±0.78	±0.37	±0.66	±2.51	±0.62	±0.91
Ca (mg per g DW)	Non-Myc	5.98	6.13	6.37	7.11	6.34	8.36
		±1.85	±1.07	±1.50	±1.11	±0.59	±0.93
	Myc	3.24	3.38	4.00	6.58	6.72	6.69
		±1.09	±0.72	±0.30	±2.66	±0.71	±1.52
Na (mg per g DW)	Non-Myc	1.51	1.08	1.34	8.02	7.69	8.38
		±1.29	±0.39	±0.36	±1.59	±1.90	±2.28
	Myc	1.35	1.18	0.89	11.09	10.38	9.48
		±0.40	±0.23	±0.24	±1.15	±0.72	±1.13
Fe (µg per g DW)	Non-Myc	128.37	136.98	120.77	145.17	150.51	196.52
		±84.47	±63.06	±18.81	±36.67	±39.84	±53.01
	Myc	89.93	141.45	118.35	91.65	88.78	88.52
		±31.47	±90.78	±31.31	±14.23	±13.62	±13.86

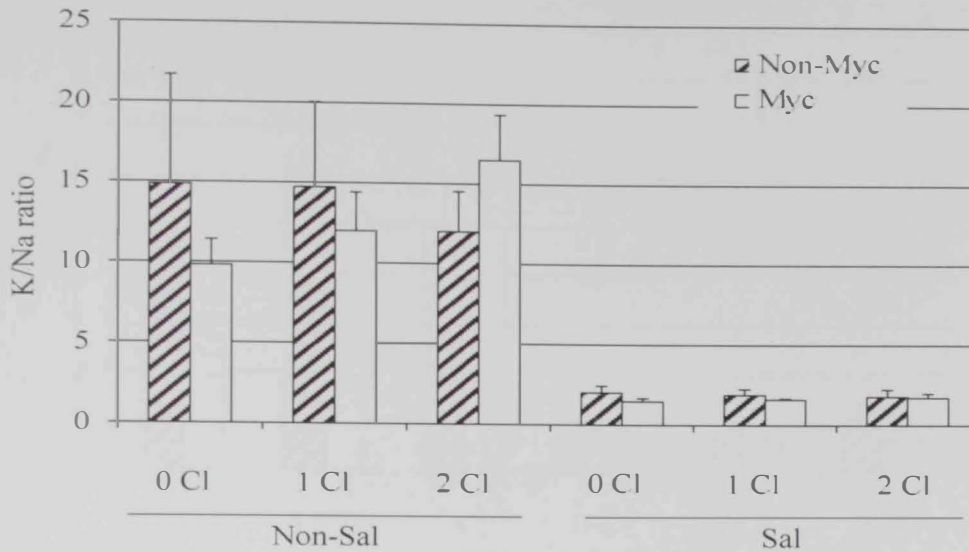
		Non-saline soil			Saline soil		
		Not clipped	1 Cl	2 Cl	Not clipped	1 Cl	2 Cl
Cu ( $\mu\text{g}$ per g DW)	Non-Myc	31.71	26.54	29.83	54.49	51.29	44.91
		$\pm 18.59$	$\pm 7.91$	$\pm 5.91$	$\pm 16.17$	$\pm 9.21$	$\pm 8.63$
	Myc	23.06	17.74	15.74	46.46	45.27	36.32
		$\pm 10.38$	$\pm 2.46$	$\pm 3.13$	$\pm 40.56$	$\pm 15.22$	$\pm 16.75$
Zn ( $\mu\text{g}$ per g DW)	Non-Myc	112.69	155.44	121.68	116.31	127.67	131.54
		$\pm 4.32$	$\pm 36.08$	$\pm 22.73$	$\pm 13.01$	$\pm 22.97$	$\pm 27.42$
	Myc	94.27	117.32	99.21	132.07	112.88	112.55
		$\pm 8.23$	$\pm 24.04$	$\pm 7.77$	$\pm 92.93$	$\pm 13.08$	$\pm 13.63$
Mn ( $\mu\text{g}$ per g DW)	Non-Myc	34.46	33.78	27.67	25.57	36.38	34.52
		$\pm 7.34$	$\pm 3.98$	$\pm 8.92$	$\pm 5.22$	$\pm 7.04$	$\pm 16.58$
	Myc	23.79	37.95	28.22	47.96	38.65	30.87
		$\pm 6.09$	$\pm 17.90$	$\pm 2.73$	$\pm 54.04$	$\pm 13.11$	$\pm 8.39$

The values are the means  $\pm$  standard deviations in mg per g dry weight for macronutrients, and in  $\mu\text{g}$  per g dry weight for micronutrients. All shoot material produced throughout the growth period was pooled into one sample, and analyzed (including the pruned and lost material). For treatment abbreviations see Fig. 26. Mean values for nonmycorrhizal plants followed by a star are significantly ( $P < 0.05$ ) different from mean values of corresponding mycorrhizal treatments (Tukey's multiple comparison).

Table 14: Results of the Three Way ANOVA performed on data obtained for element concentrations in the shoots of Sudan grass plants.

	ANOVA								Interaction Factor
	Myc		Sal		Cl		Interactions		
	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	
P	<b>&lt;0.001</b>	32.157	0.154	2.133	0.342	1.110	<b>0.002</b>	11.345	Myc X Sal
K	0.935	0.00667	<b>0.018</b>	6.220	0.746	0.296	<b>&lt;0.001</b>	16.209	Myc X Sal
Mg	<b>0.054</b>	3.976	<b>&lt;0.001</b>	14.093	0.664	0.415			
Ca	<b>&lt;0.001</b>	17.483	<b>&lt;0.001</b>	30.116	0.267	1.375	<b>0.014</b>	6.812	Myc X Sal
Na	<b>0.007</b>	8.409	<b>&lt;0.001</b>	474.960	0.540	0.628	<b>0.002</b>	11.314	Myc X Sal
Fe	<b>0.009</b>	7.736	0.788	0.0734	0.635	0.460			
Cu	0.057	3.883	<b>&lt;0.001</b>	23.812	0.458	0.800			
Zn	0.084	3.166	0.556	0.353	0.377	1.005			
Mn	0.618	0.253	0.356	0.877	0.570	0.571			

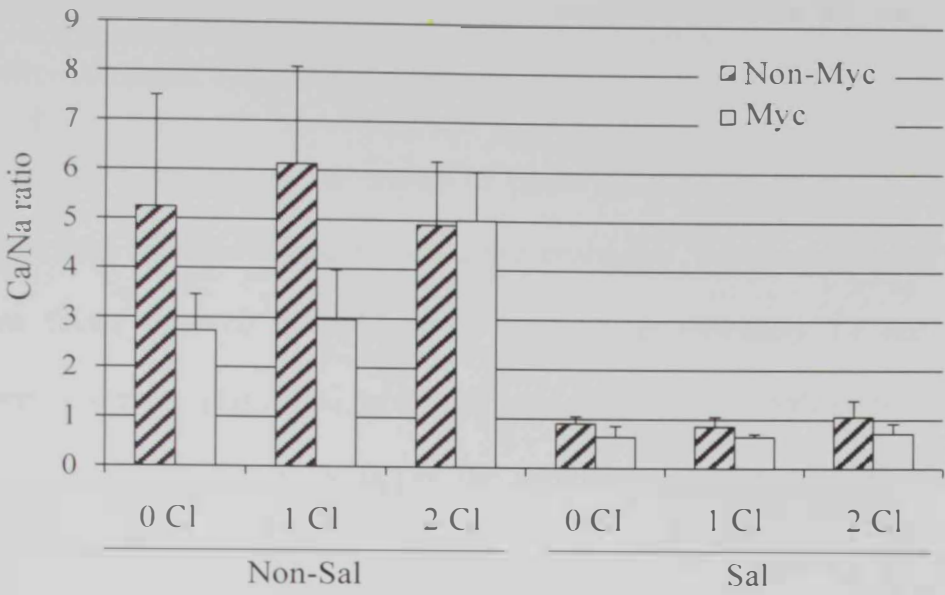
For treatment abbreviations see Fig. 26. P values indicative of a significant ( $P<0.05$ ) influence of mycorrhizal inoculation (Myc), salt application (Sal), clipping (Cl), or an interaction between factors are printed in bold letters.



Factor	P-Value
Mycorrhizal inoculation (Myc)	0.411
Saline (Sal)	<b>&lt; 0.001</b>
Clipping (Cl)	0.640
Interaction (Myc x Cl)	<b>0.048</b>

Figure 35: K/Na ratio in shoot material obtained from Sudan grass plants. The values are the means  $\pm$  standard deviations. All shoot material produced throughout the growth period was pooled into one sample, and analyzed (including the pruned and lost material). For treatment abbreviations see Fig. 26. The table shows the results of the Three Way ANOVA. P-values indicating a significant effect of mycorrhizal root inoculation (Myc), soil salinity (Sal) or plant clipping (Cl) ( $P < 0.05$ ) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line.





Factor	P-Value
Mycorrhizal inoculation (Myc)	< 0.001
Saline (Sal)	< 0.001
Clipping (Cl)	0.361
Interaction (Myc x Sal)	0.014

Figure 36: Ca/Na ratio in shoot material obtained from Sudan grass plants. The values are the means  $\pm$  standard deviations. All shoot material produced throughout the growth period was pooled into one sample, and analyzed (including the pruned and lost material). For treatment abbreviations see Fig. 26. The table shows the results of the Three Way ANOVA. P-values indicating a significant effect of mycorrhizal root inoculation (Myc), soil salinity (Sal) or plant clipping (Cl) ( $P < 0.05$ ) are printed in bold. Significant ( $P < 0.05$ ) interactions are given in the last line.

Clipping did not affect total shoot uptake of P, K, Mg and Na. Exposure of roots to soil salinity decreased the shoot uptake of P, K and Mg in both, mycorrhizal and nonmycorrhizal plants (Tables 15 and 16). Mycorrhiza fungal inoculation increased the shoot uptake of P, K and Mg, but the relative net contribution of the mycorrhiza

symbiosis to shoot uptake of these elements tended to be larger for plants growing on saline compared with the non-saline soil.

Sodium contents in shoots of plants growing on saline soil were higher compared with corresponding non-saline treatments. In response to salt application, Na uptake into the shoot increased between approximately 1.7 and 3.0 fold in nonmycorrhizal plants, and between 2.5 and 5.0 fold in mycorrhizal treatments. Shoot Na uptake was generally larger for mycorrhizal compared with corresponding nonmycorrhizal treatments.

Clipping did not affect total shoot uptake of Micronutrients. Soil salinity decreased the shoot uptake of Cu, Zn, Fe and Mn in both, mycorrhizal and nonmycorrhizal plants. Shoot Cu, Zn, Fe and Mn uptake was larger for mycorrhizal compared with nonmycorrhizal treatments.

Table 15: Element content in shoot material obtained from Sudan grass plants in mg per plant.

		Non-saline soil			Saline soil		
		Not clipped	1 Cl	2 Cl	Not clipped	1 Cl	2 Cl
P (mg per plant)	Non-Myc	5.78 *	7.25 *	6.00 *	1.67	2.74	1.21
		±3.35	±2.79	±6.00	±0.57	±0.91	±0.54
	Myc	19.86	26.10	20.67	13.51	9.24	10.46
		±4.81	±11.88	±3.62	±5.16	±3.01	±3.15
K (mg per plant)	Non-Myc	72.99	106.69 *	93.14	33.45	33.22	22.82
		±22.93	±48.11	±96.85	±10.89	±11.59	±7.21
	Myc	199.56	277.18	229.62	160.32	95.08	105.11
		±15.16	±97.28	±16.32	±73.17	±44.89	±32.68
Mg (mg per plant)	Non-Myc	26.15 *	43.23 *	34.17 *	13.87	15.02	12.03
		±4.38	±15.48	±30.46	±2.84	±4.60	±3.62
	Myc	72.56	92.82	83.44	58.51	41.10	42.65
		±4.12	±28.75	±17.67	±20.92	±21.83	±10.93
Na (mg per plant)	Non-Myc	5.39	7.63	7.15	16.56 *	18.63	12.84 *
		±1.39	±2.87	±5.95	±2.69	±8.29	±1.67
	Myc	21.97	23.76	14.39	108.83	59.60	63.20
		±3.69	±8.79	±2.54	±53.43	±27.50	±25.46
Fe (mg per plant)	Non-Myc	0.72	0.91	0.83	0.32	0.34	0.31
		±0.79	±0.22	±1.01	±0.14	±0.04	±0.10
	Myc	1.52	2.75	1.99	1.17	0.51	0.59
		±0.68	±3.07	±0.79	±0.29	±0.27	±0.23
Cu (mg per plant)	Non-Myc	0.12 *	0.18	0.16	0.13 *	0.12	0.07
		±0.04	±0.05	±0.14	±0.07	±0.05	±0.02
	Myc	0.36	0.35	0.26	0.33	0.23	0.21
		±0.08	±0.09	±0.02	±0.12	±0.03	±0.02
Zn (mg per plant)	Non-Myc	0.55	1.08 *	0.82	0.26	0.31	0.21
		±0.25	±0.27	±0.97	±0.11	±0.13	±0.09
	Myc	1.57	2.50	1.63	1.00	0.63	0.75
		±0.20	±1.22	±0.08	±0.09	±0.23	±0.34

Mn (mg per plant)	Non-Myc	0.16 ±0.06	0.24 * ±0.07	0.17 ±0.19	0.06 ±0.03	0.09 ±0.04	0.05 ±0.02
	Myc	0.39 ±0.03	0.79 ±0.54	0.46 ±0.03	0.30 ±0.16	0.20 ±0.05	0.21 ±0.10

The values are the means ± standard deviations. All shoot material obtained throughout the growth period and at the time of harvest was analyzed. For treatment abbreviations see Fig. 26. Mean values for nonmycorrhizal plants followed by a star are significantly ( $P < 0.05$ ) different from mean values of corresponding mycorrhizal treatments (Tukey's multiple comparison).

Table 16: Results of the Three Way ANOVA performed on data obtained for element content in the shoots of Sudan grass plants.

	ANOVA								Interaction Factor
	Myc		Sal		Cl		Interactions		
	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	
P	<0.001	74.016	<0.001	28.704	0.601	0.517	0.029	5.247	Myc X Sal
K	<0.001	57.995	<0.001	32.715	0.691	0.374			
Mg	<0.001	65.071	<0.001	30.634	0.631	0.467			
Na	<0.001	48.018	<0.001	38.192	0.114	2.323	<0.001	19.826	Myc X Sal
Fe	0.006	8.629	0.004	9.990	0.809	0.213			
Cu	<0.001	54.140	0.012	7.144	0.067	2.940			
Zn	<0.001	28.286	<0.001	29.672	0.219	1.591			
Mn	<0.001	23.121	<0.001	15.799	0.195	1.716			

For treatment abbreviations see Fig. 26. P values indicative of a significant ( $P < 0.05$ ) influence of mycorrhizal inoculation (Myc), salt application (Sal), clipping (Cl), or an interaction between factors are printed in bold letters.

Similar with P concentrations in shoots, concentrations of P in root tissues were slightly higher in mycorrhizal compared with nonmycorrhizal plants (Tables 17 and

18). However, there was no effect of soil salinity on root P concentrations. Roots of plants clipped two times had higher P concentrations compared with those of corresponding non-clipped controls. One time clipping had no effect on P concentrations in the roots.

Concentrations of K and Mg were generally lower in roots that grew in saline compared with non-saline soil, but there was no effect of mycorrhiza fungal inoculation or clipping. The Na concentrations in roots were higher when they grew in saline compared with non-saline soil. Soil salinity, but not clipping or mycorrhiza fungal inoculation affected root Na concentrations.

Concentrations of P were in a similar range in shoots and roots of the plants of this experiment. Mg and Ca concentrations were higher in roots compared with those in shoots across all treatments.

Table 17: Element concentrations in root material obtained from Sudan grass plants.

		Non-saline soil			Saline soil		
		Not clipped	1 CI	2 CI	Not clipped	1 CI	2 CI
P (mg per g DW)	Non-Myc	0.87	0.89	1.03	0.95	0.91	1.17
		±0.16	±0.22	±0.15	±0.12	±0.15	±0.28
	Myc	1.22	1.04	1.41	1.14	1.13	1.20
		±0.07	±0.22	±0.10	±0.24	±0.07	±0.09
K (mg per g DW)	Non-Myc	13.67	13.47	9.97	7.81	8.49	7.04
		±3.99	±2.95	±3.73	±3.15	±3.78	±2.00
	Myc	12.65	10.86	13.28	6.30	4.18	5.78
		±0.39	±4.22	±2.57	±4.41	±1.23	±3.38
Mg (mg per g DW)	Non-Myc	13.72	13.76	14.52	13.44	11.99	10.52
		±1.15	±2.31	±1.93	±1.26	±1.23	±1.78
	Myc	13.95	15.35	13.69	11.73	12.30	12.38
		±2.87	±3.53	±3.03	±3.05	±3.52	±2.42
Ca (mg per g DW)	Non-Myc	15.58	17.79	19.22	24.20	17.30	16.63
		±4.09	±6.93	±3.21	±3.60	±3.40	±3.54
	Myc	16.47	19.12	14.00	13.89	18.59	18.07
		±4.99	±3.57	±2.25	±4.07	±2.74	±5.03
Na (mg per g DW)	Non-Myc	4.09	3.87	3.97	8.61	8.71	8.16
		±0.68	±0.10	±0.71	±1.96	±2.14	±3.13
	Myc	4.68	4.64	4.60	9.98	8.74	8.73
		±0.80	±1.52	±0.37	±1.01	±1.17	±1.28

The values are the means ± standard deviations in mg per g dry weight. All root material obtained at the time of harvest was analyzed. For treatment abbreviations see Fig. 26. The mean values did not significantly differ ( $P < 0.05$ ; Tukey's multiple comparison).



Table 18: Results of the Three Way ANOVA performed on data obtained for element concentrations in the root of Sudan grass plants.

	ANOVA							
	Myc		Sal		Cl		Interactions	
	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value
P	<b>&lt;0.001</b>	20.772	0.877	0.0243	<b>0.003</b>	6.682		
K	0.191	1.773	<b>&lt;0.001</b>	38.064	0.605	0.510		
Mg	0.738	0.113	<b>0.006</b>	8.591	0.796	0.229		
Ca	0.148	2.190	0.369	0.828	0.708	0.349	<b>0.014</b>	4.790
Na	0.132	2.381	<b>&lt;0.001</b>	111.488	0.646	0.443		

For treatment abbreviations see Fig. 26. P values indicative of a significant ( $P<0.05$ ) influence of mycorrhizal inoculation (Myc), the salinity treatment (Sal), clipping (Cl), or an interaction between factors are printed in bold letters.

Root contents of P, K and Mg were lower on saline compared with non-saline soil (Tables 19 and 20). Mycorrhiza inoculation increased the amount of these elements in roots. Irrespective of the salinity treatment, the relative net contribution of mycorrhiza fungal colonization to root P content was smaller for the 1 Cl treatment compared with that of the corresponding 2 Cl and control treatments.

The root contents of K, Mg and Na showed relatively high variability within the same treatment. Different from the shoots, roots of the salinity treated plants did not contain different amounts of Na compared with the corresponding non-treated controls. Mycorrhiza inoculation, however, increased Na contents in the roots

compared with nonmycorrhizal controls. Clipping had no effect on the root P, K, Mg and Na contents.

Table 19: Element content in root material obtained from Sudan grass plants in mg per plant.

		Non-saline soil			Saline soil		
		Not clipped	1 Cl	2 Cl	Not clipped	1 Cl	2 Cl
P (mg per plant)	Non-Myc	2.54 *	4.76	3.85 *	1.33	2.23	1.65
		±1.71	±2.12	±3.84	±0.73	±0.88	±1.20
	Myc	10.44	8.19	12.94	4.87	3.39	5.50
		±1.85	±3.13	±1.51	±2.79	±2.14	±3.81
K (mg per plant)	Non-Myc	39.67	67.39	45.77 *	12.04	23.06	10.31
		±21.43	±12.74	±58.41	±7.40	±17.95	±8.19
	Myc	107.89	95.80	122.26	28.14	13.56	31.59
		±16.43	±53.97	±26.01	±24.14	±10.72	±32.19
Mg (mg per plant)	Non-Myc	38.10 *	72.84	48.99	19.20	29.91	14.93
		±21.43	±26.63	±37.13	±10.63	±12.40	±10.31
	Myc	116.41	128.84	125.53	51.47	38.37	58.69
		±10.15	±64.72	±27.09	±33.83	±25.51	±42.86
Na (mg per plant)	Non-Myc	11.83	20.01	16.07	12.79	23.00	10.08
		±6.98	±5.57	±17.25	±8.77	±13.43	±3.83
	Myc	39.40	40.87	42.22	40.30	27.34	41.12
		±5.34	±21.78	±4.54	±16.27	±20.23	±31.85

The values are the means ± standard deviations. All root material obtained at the time of harvest was analyzed. For treatment abbreviations see Fig. 26. Mean values for nonmycorrhizal plants followed by a star are significantly ( $P < 0.05$ ) different from mean values of corresponding mycorrhizal treatments (Tukey's multiple comparison).

Table 20: Results of the Three Way ANOVA performed on data obtained for element content in the root of Sudan grass plants.

	ANOVA								
	Myc		sal		Cl		Interactions		Interaction Fraction
	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	P-Value	F-Value	
P	<b>&lt;0.001</b>	49.852	<b>&lt;0.001</b>	33.546	0.228	1.541	<b>0.006</b>	8.363	Myc X Sal
							<b>0.040</b>	3.538	Myc X Cl
K	<b>&lt;0.001</b>	16.048	<b>&lt;0.001</b>	51.493	0.864	0.147	<b>0.006</b>	8.378	Myc X Sal
Mg	<b>&lt;0.001</b>	30.133	<b>&lt;0.001</b>	34.968	0.599	0.520	<b>0.024</b>	5.516	Myc X Sal
Na	<b>&lt;0.001</b>	26.423	0.559	0.348	0.948	0.0540			

For treatment abbreviations see Fig. 26. P values indicative of a significant ( $P < 0.05$ ) influence of mycorrhizal inoculation (Myc), salt application (Sal), clipping (Cl), or an interaction between factors are printed in bold letters.

### 3.4 Discussion

#### 3.4.1 Effect of soil salinity on the relative contribution of the arbuscular mycorrhiza fungal symbiosis to plant growth and nutrient uptake

Soil salinity negatively affected plant growth across all clipping and inoculation treatments in the present experiment. Both, shoot length expansion and leaf formation were lower in salinity treated plants compared with the respective controls around one month after the salinity treatments were established. The dry weight of the plants produced throughout the experiment period decreased by more than half in response to the saline treatment, irrespective of mycorrhiza fungal inoculation. This suggests that Sudan grass responds with considerable growth depression to moderate levels of soil salinity. With respect to dry weight partitioning, an increase in the lost biomass, and a decrease in the flower and seed biomass was generally observed in response to soil salinity.

There are three principal mechanisms by which soil salinity may negatively affect plant growth. On a saline soil the osmotic soil potential is low, and this can make it difficult for plants to acquire water (Munns et al., 2006). High levels of Na and Cl may also have a direct negative effect on the physiology and functioning of plant cells, when they are present in the cytoplasm in amounts exceeding a specific threshold value (Dagar and Tomar, 2002; Badda et al., 2014; Sinclair et al., 2014). High concentrations of  $\text{Na}^+$  and  $\text{Cl}^-$  may further disbalance plant ion uptake (Hasegawa et al., 2000; Munns et al., 2006). Competition of  $\text{Na}^+$  and  $\text{K}^+$  or  $\text{Ca}^{2+}$  for uptake sites is relatively common, and may result in Na induced K or Ca deficiency on saline or sodic soils (Rabie, 2005). In addition to ion competition for uptake sites, a decreased mass flow towards the root surface, and a decline in integrity and polarization of root cell plasmamembranes can

also contribute to a poorer nutritional status of plants growing in saline compared with non-saline soil. Arbuscular mycorrhizal fungi have often been shown to contribute to growth of plants growing on saline soil, even though the precise mechanisms are not yet completely understood (Estrada et al., 2013a). Arocaa et al. (2013) observed that when exposed to saline soil, mycotrophic plants may increase the strigolactone production to stimulate the branching and root colonization by symbiotic arbuscular mycorrhizal fungi. This suggests that some plant species may become more dependent on their fungal partner under salinity stress.

In the present experiment, arbuscular mycorrhiza fungal inoculation increased the dry weight of Sudan grass, irrespective of whether the soil was saline, or not. The relative contribution of the fungal symbiosis to plant dry weight production did not differ depending on whether host plants grew on saline or non-saline soil. On one hand, these results indicate that the presence of arbuscular mycorrhizal fungi can help prevent yield decline on saline soils. On the other hand, the results of the present study do not support the idea that the relative contribution of the mycorrhiza symbiosis to plant growth increases when plants are affected by salt stress. Positive effects of mycorrhiza inoculation on plant performance have also been observed previously, e.g. by Al-Karaki et al. (2001), Daei et al. (2009) and Al-Khaliel (2010). When exposed to saline soil, mycorrhiza inoculation has been shown to improve the growth of onion (Hirrel and Gerdemann, 1980; Ojala et al., 1983), citrus seedlings (Wu et al., 2010), maize (Feng et al., 2002; Sheng et al., 2008), lettuce (Jahromi et al., 2008) and tomato (Al-Karaki, 2000).

Arbuscular mycorrhizal fungi can be adapted to, and grow in saline substrates (Wilde et al., 2009). It has been shown that arbuscular mycorrhizal fungi originating

from saline habitats are particularly efficient in contributing to plant growth under salinity (Zhu, 2001; Ruiz-Lozano et al., 2012). In the present study, there was no difference in the extent of arbuscular mycorrhiza fungal root colonization between plants that grew on saline and non-saline soil. Results obtained by Hartmond et al. (1987) and Wu et al. (2010) confirm the results of the present experiment. Irrespective of the soil salinity, root colonization rates were very high. This suggests that there was no negative effect of soil salinity on intraradical mycorrhiza development. However, it needs to be considered that the technique used for staining and observation of intraradical fungal structures in the present study did not allow for distinction between live and dead fungal tissues. Thus it can not be excluded that there were differences in the proportion of the live fungal structures within the roots of the salinity treated and non-treated plants.

Adaptation of plants to a saline growth substrate involves mechanisms that require additional energy, e.g. the uptake and release of  $\text{Na}^+$  and  $\text{Cl}^-$  (Chen et al., 2007), or the synthesis of compatible solutes for osmotic adjustment (Moghaieb et al., 2004). At the same time, the photosynthetic capacity of plants that grow under salinity stress is often reduced. The results of the present experiment do not suggest that the extent of arbuscular mycorrhiza fungal root colonization or the relative contribution of the symbiosis to plant performance decline under salt stress due to a decreased ability of the host plant to supply the fungal symbiont with carbohydrates.

In the present study, soil salinity decreased the shoot/root ratio. A stronger decline in shoot compared with root growth is a common observation in plants exposed to salinity (Lauchli and Grattan, 2007; Munns and Tester, 2008). A reason could be that under salinity it is easier for a plant to sustain the turgor in root compared with



shoot cells. The shoot/root ratio strongly depends on the plant water and nutrient supply status (Munns and Tester, 2008; Garg and Pandey, 2015). Under salinity the plant nutritional status is often decreased, leading to increased photoassimilate investment into root proliferation and foraging for soil nutrient pools. In the present study, plants that grew under soil salinity took up less P, K and Mg, Zn and Mn compared with corresponding controls grown in non-saline soil.

Across all treatments, arbuscular mycorrhiza root colonization increased the shoot/root ratio. The reason for this could be an improved nutritional status of mycorrhizal plants. In mycorrhizal plants, P uptake via the symbiotic pathway can account for almost 100 % of the total P taken up (Pearson and Jakobsen, 1993; Smith et al., 2003; Poulsen et al., 2005). Mycorrhizal plants may thus rather invest carbohydrates into supplying the fungal symbiont, than the production of additional root biomass.

Under salinity, the relative contribution of mycorrhiza fungal root colonization to shoot P uptake seemed to be larger compared with plants that grew in non-saline soil. While mycorrhiza inoculated plants took up on an average 3.5 times more P into their shoots compared with nonmycorrhizal controls under non-saline conditions, the mycorrhizal symbiosis improved shoot P contents on an average by a factor of 6.6 when plants grew on saline soil. This finding supports earlier reports of (Hirrel and Gerdemann, 1980; Ojala et al., 1983; Al-Karaki, 2000; Al-Khaliel, 2010) who found that contribution to P uptake from saline soil may be a main mechanism by which the mycorrhizal symbiosis contributes to plant performance under salinity. Compared with standard values cited by Bergmann (1992) the shoot P concentrations were in a very

low range in all plants involved in this experiment. Results suggest that P deficiency occurred, and that P supply was a growth limiting factor.

When the plant P nutritional status is improved due to mycorrhiza fungal contribution to plant P uptake, this may also positively affect the ability of the host plant to acquire other nutritional elements via the asymbiotic pathway. Reasons for this could lie, e.g. in an increased photosynthetic capacity of the host plant (Smith and Read, 1997), and/or improved root growth physiological functioning. The extraradical hyphal network might also improve soil structure, and the quality of contact between root surface and rhizosphere soil (Johnson et al., 2010).

It may be possible that mycorrhizal fungi native to saline ecosystems would have contributed even more to plant P uptake from saline soil compared with the fungi used for inoculation in the present study, which originated from a non-saline habitat.

The mechanisms by which the mycorrhiza fungal symbiosis contributed to the shoot uptake of elements other than P remains speculative. Similar with P, K concentrations in the shoots of all plants were indicative of deficiency. The mycorrhiza fungal contribution to uptake of P and K might thus have been a main reason for an increased dry weight production of mycorrhizal compared with nonmycorrhizal plants under saline as well as non-saline conditions. The ability of the arbuscular mycorrhizal symbiosis to enhance the ability of host plants to absorb K from saline soil have been reported by many researchers (Mohammed et al., 2003; Alguacil et al., 2003; Zandavalli et al., 2004; Rabie and Almadini, 2005; Giri et al., 2007; Sharifi et al., 2007; Zuccarini and Okurowska, 2008; Porras- Soriano et al., 2009; Kaya et al., 2009; Wu et al., 2010; Talaat and Shawky, 2011; Mardukhi et al., 2011), but the mechanisms behind this are still speculative.

In mycorrhizal plants, not only K, but also Na uptake increased compared with nonmycorrhizal plants. This effect was particularly evident under elevated NaCl levels in the soil. The shoot K/Na ratio did thus not differ between mycorrhizal and nonmycorrhizal plants. Maintenance of the same K/Na ratios between shoots of mycorrhizal and nonmycorrhizal plants might be a hint that both elements were taken up by plant transporters in both cases. However, this remains speculative. In both, mycorrhizal and nonmycorrhizal plants, K/Na ratios were low under saline conditions, making the occurrence of Na induced K deficiency likely (Evelin et al., 2009). Our study does not confirm the idea that mycorrhiza fungal root colonization increases the uptake selectivity for K (Rinaldelli and Mancuso, 1996; Tian et al., 2004; Rabie and Almadini, 2005).

Cantrell and Linderman (2001) showed that mycorrhizal contributed in increased  $\text{Ca}^{2+}$  uptake in lettuce. Hammer et al. (2011) found that arbuscular mycorrhizal fungi take up the nutrients from the soil selectively for example  $\text{K}^+$  and  $\text{Ca}^{2+}$ . Whether such contributions are due to direct uptake via the mycorrhizal hyphae, or indirect effects of an improved P nutrition, deserves further investigation.

In the current experiment, the results indicate that Ca concentrations the shoots were lower in mycorrhizal plants compared to those in nonmycorrhizal plants. Some researchers found the opposite, and reported that Ca concentrations in mycorrhizal plants were higher than those in nonmycorrhizal controls (Yano-Melo et al., 2003). However, differences in Ca concentrations in plant shoots can also be due to differences in growth, and corresponding dilution effects. The Ca/Na ratio was even decreased by mycorrhiza fungal inoculation, even though values were not in a critical range for plants that grew in saline or non-saline soil.

Na concentrations in the shoots of plants exposed to salinity were in a range that is still tolerated by moderately salt tolerant plants (Bergmann, 1992). The negative impact of salinity on plant growth observed in the present study might thus have been rather due to Cl toxicity, or a negative impact of NaCl on uptake of nutrients and water.

Numerous previous studies suggest that mycorrhiza fungal root colonization can decrease overall uptake of Na into the plant shoot (Dixon et al., 1993; Giri and Mukerji, 2004; Murkute et al., 2006; Ghazi and Al-Karaki, 2006; Sharifi et al., 2007; Zuccarini and Okurowska, 2008; Kohler et al., 2009; Kaya et al., 2009; Porras-Soriano et al., 2009; Khalil et al., 2011; Hammer et al., 2011; Cekic et al., 2012; Talaat and Shawky, 2014). Our results, however, can not confirm this.

Mycorrhizal fungi are known to assist plants to grow by contributing to their net nutrient uptake. In the present study, mycorrhizal plants had higher contents of K, Mg, Cu, Zn and Mn in the shoot compared with the corresponding nonmycorrhizal controls, irrespective of whether the growth substrate was saline or not. The relative contribution of the mycorrhizal symbiosis to shoot uptake of these elements did not differ depending on soil salinity, suggesting that the functioning of the symbiosis was not negatively affected by elevated levels of NaCl in the rooting zone.

Levels of Mg were in a sufficient range in mycorrhizal as well as nonmycorrhizal shoots. An increase in Mg uptake in response to mycorrhiza root colonization has been reported by some researchers (Marschner and Dell, 1994; Raghothama, 2000; Giri et al., 2003; Giri and Mukerji 2004; Murkute et al., 2006; Miransari et al., 2009a,b ; Wu et al., 2010; Khalil et al., 2011; Cekic et al., 2012; Talaat and Shawky, 2014).



In this experiment, the results suggest that the mycorrhiza fungal symbiosis also helped to enhance plant performance by increasing P concentrations in the roots of mycorrhizal plants compared to those in nonmycorrhizal plants when grown in saline and non-saline soil. But, it seems that the mycorrhizal inoculation had no effect on K, Mg and Ca concentrations in the roots of plants which were grown under saline and non-saline conditions. Element concentrations in mycorrhizal roots are difficult to interpret, as partitioning of elements between root tissues and fungal mycelia is unknown.

Arbuscular mycorrhizal fungi can also improve Fe, Cu and Mn uptake of plants (Marschner and Dell, 1994; Miransari et al., 2006). The micronutrient concentrations in shoots of Sudan grass plants of the present study were in a sufficient range, with Zn, Cu and Fe concentrations being above optimal values, but not yet in a toxic range. Mycorrhiza inoculation increased uptake of Zn, Mn, Cu and Fe in the present study. The Fe concentrations in the tissues of mycorrhizal plants were lower compared with those in nonmycorrhizal controls. Whether this was due to a concentration effect, or a protective mechanism that prevented mycorrhizal plants from taking up excessive amounts of this element (Nogueira et al., 2004; Davies et al., 2005; Cardoso and Kuyper, 2006; Miransari et al., 2006) remains speculative.

Kothari et al. (1991) reported that Zn was taken up and transported via arbuscular mycorrhizal hyphae. Some studies reported that the phosphates (P) increased the uptake of Zn in *Sedum alfredii* plant because of increasing in Zn concentration of shoots and dry matter yield. The P fertilizer with multiple clippings of plants at the same time can help in the removal of Zn from contaminated soils (Huang et al., 2012).

Levels of nitrogen remain unknown as the tissue concentrations of this element were not analyzed in the present study. Thus, it can not be excluded that the mycorrhiza symbiosis also contributed to the uptake of this element from saline and/or non-saline soil.

Arbuscular mycorrhizal fungi may contribute to plant uptake of nutritional elements either directly by transferring acquired elements to the plant cytoplasm at the symbiotic interface, or indirectly by improving the ability of the roots to take up nutrients. Though mycorrhizal fungi have been shown to contribute to plant uptake of a wide range of nutritional elements (Rillig, 2004), studies have only confirmed hyphal transport and transfer to the plant of P, N, Zn and Cu so far.

### **3.4.2 Effect of shoot clipping on the relative contribution of the arbuscular mycorrhiza fungal symbiosis to plant growth and nutrient uptake**

In groundcovers, the removal of shoot biomass by mowing or clipping is a common practice. The consequences for the mycorrhiza fungal symbiosis might be transient when plants re-establish quickly (Torresa et al., 2011). On one hand, the mycorrhizal fungi might assist plant re-establishment by contributing to nutrient uptake. On the other hand, the fungus might delay re-establishment as it competes with plant organs for photoassimilates. Smith and Read (1997) showed that arbuscular mycorrhizal root colonization, after clipping the plants, had a positive effect on uptake of nutrients by plants, as well as on plant re-growth (Newingham, 2002). Hetrick et al. (1990), Gange et al. (2002), Klironomos et al. (2004) and Wearn and Gange (2007) reported that host plant grazing had a negative effect on arbuscular mycorrhizal fungi development. According to Jirout et al. (2009) and Ba et al. (2012) the arbuscular mycorrhizal fungi diversity and colonization were increased under light and moderate



defoliation, and decreased under extremely strong grazing. Several previous studies reported that defoliation can reduce arbuscular mycorrhizal spore abundance (Eom et al., 2001; Su and Guo, 2007; Tian et al., 2009). Reduction in leaf area by clipping can reduce the amount of carbohydrates available to roots (Richards, 1984; Trent et al., 1987). Medina-Roldán et al. (2008) and Barto and Rilling (2010) reported that the carbon limitation caused the negative effect of heavy defoliation on arbuscular mycorrhizal colonization. When photosynthetically active tissues are removed from the shoot, associated arbuscular mycorrhizal fungi might suffer from carbohydrate deficiency (Paul and Kucey, 1981). However, other studies have shown different responses of arbuscular mycorrhizal fungi colonization to clipping. There are previous reports (Reece and Bonham, 1978; Walling and Zabinski, 2006; Tian et al., 2009; Torresa et al., 2011), which found that the arbuscular mycorrhizal root colonization did not decrease in response to host defoliation. Davidson and Christensen (1977) and Reece and Bonham (1978) reported that the frequency of arbuscular mycorrhizal colonization in different perennial tussock grasses was not affected by grazing. Similarly, in the present experiment, shoot clipping had no effect on the extent of mycorrhiza fungal root colonization. It is possible that this was because the mycorrhizal fungi responded to the clipping short-term, and established back to the control values when host plants recovered (Torresa et al., 2011). It is also possible that the clipping effect depends on the arbuscular mycorrhiza fungal species (Klironomos et al., 2004). Torresa et al. (2011) suggested that when plant photosynthetic area re-establishes quickly after clipping, the mycorrhizal colonization might not decrease much, as carbohydrate supply is quickly restored. When the mycorrhizal symbiosis is already sufficiently established by the time of clipping, the fungal contribution to nutrient uptake might well contribute to a quick re-establishment of the clipped shoots.

In accordance, Wu et al. (2011) showed that after cutting there was an increase in arbuscular mycorrhiza root colonization of bermudagrass, and mycorrhizal plants showed a higher dry weight compared to nonmycorrhizal controls. The authors found that mycorrhizal plants recovered faster from clipping than nonmycorrhizal ones. As opposed to the above results, Walling and Zabinski (2006) showed that arbuscular mycorrhizal plants were smaller compared to nonmycorrhizal controls, and this effect was more pronounced when plants were clipped. Wu et al. (2011) suggested that the different effects of clipping on arbuscular mycorrhizal colonization are related to differences between plant species. Walling and Zabinski (2006) reported that *Cenaurea masculosa* had greater compensatory growth after defoliation compared with *Festuca idahoensis* and *Pseudoroegneria spicata*. That might be because of its high competitive strength (Marler et al., 1999). The latter is most likely at least partially conferred by the mycorrhizal symbiosis (Carey et al., 2004), and thus good exploitation of soil P resources (Zabinski et al., 2002). After two consecutive years of defoliation, *Paspalum vaginatum* had higher rates of arbuscular mycorrhizal root colonization than the genotypes of *Aristida* and *Sporobolus cryptandrus* (Torres et al., 2011). Moreover, Walling and Zabinski (2006) reported that there was no evidence that the arbuscular mycorrhizal colonization would encourage a greater compensatory growth of plants after clipping, and provided evidence that the arbuscular mycorrhizae do not always assist their host plants, and may even decrease the competitive strength of plants under certain conditions.

Competition between arbuscular mycorrhizal fungi and their host plants for photoassimilates might play a more important role under salinity. Usually plants exposed to saline soil have been shown to benefit from the arbuscular mycorrhizal symbiosis. However, plant adaptations to saline soil require energy in form of

carbohydrates, e.g. for active efflux of unwanted ions, synthesis of compatible solutes or compartmentalization of  $\text{Na}^+$  and  $\text{Cl}^-$ . It is thus possible that under conditions of limited photosynthesis, competition between plants and arbuscular mycorrhizal fungi for photoassimilates is particularly strong on saline soils.

A reason why clipping had no effect on plant growth, mycorrhiza development and nutrient uptake. In the present experiment might be that the frequency and/or intensity of clipping in the present study was not very high. It is possible that some effects of clipping on mycorrhiza development were overlooked, as the extent of root colonization, but not the abundance of individual fungal structures was observed. In a study by Klironomos et al. (2004), intraradical hyphae and arbuscules were negatively affected by clipping, whereas the production of vesicles and spores was enhanced, and the extraradical hyphal length remained unaffected. Also, the way of interacting the arbuscular mycorrhizal fungi with the host plants depend on the species of arbuscular mycorrhizal fungi (Sanders and Fitter, 1992; Klironomos, 2003).

Soil salinity decreases the osmotic potential in the rhizosphere, which may make it more difficult for plants to take up water from the soil. Mass flow of  $\text{NaCl}$  into the rhizosphere increases with increasing plant transpiration. It could be speculated that removal of leaf biomass reduced transpiration in Sudan grass plants, and with it mass flow of  $\text{NaCl}$  into the rhizosphere. Removal of leaf mass might also have reduced total plant water demand.

## Conclusions

The results of the present study indicate that *C. conglomeratus* plants have a considerable potential for biomass production under conditions of the UAE. The observation that a sedge adapted to grow under some of the most adverse abiotic conditions is able to respond with considerable biomass production to input of additional irrigation water and fertilizer, suggests a high ecological plasticity. Whether this is unique among the UAE native flora, or there are other species exhibiting such growth potential, deserves further investigation.

In the present study, *C. conglomeratus*, a native non-host to arbuscular mycorrhizal fungi, outperformed a mycotrophic introduced crop. Should future studies confirm this finding for a wider range of agricultural soils of the UAE, screening for genotypes for biomass and/or animal fodder production would possibly need to involve more native plants and members of the Cyperaceae. So far, most grasses used for animal feed production in the UAE and elsewhere are members of the Poaceae.

The precise mechanisms by which *C. conglomeratus* mobilizes nutritional elements from the soil deserve further investigation. Rhizosphere acidification might play a role, as well as association with beneficial rhizosphere microorganisms. Though the field experiment conducted involved two different irrigation treatments, the results of the present study do not allow for unequivocal conclusions on the comparative performance of *C. conglomeratus* and Sudan grass under water limitation. Future studies would need to involve water supply treatments with lower amounts of water provided.



In the field experiment that was conducted, *C. conglomeratus* and Sudan grass plants were cultivated for a period of 7 months. While Sudan grass is relatively easily established from seeds, *C. conglomeratus* propagation proved most successful from rhizome cuttings. This mode of propagation is relatively time consuming, and requires the availability of larger amounts of cuttings for pasture establishment. Economical feasibility of *C. conglomeratus* stands would possibly require that the pastures could be used for several consecutive years for biomass production. Monitoring of plant yields over a longer period of time would thus be required before clear recommendations on the use of *C. conglomeratus* in UAE agriculture can be made.

Similar with some previous reports, results of this study suggest that when grown with roots sharing the same planting pot, mycorrhizal root systems may negatively affect the development and functioning of neighboring non-host roots. The present study can, however, not confirm such observations under field conditions. The relevance of direct negative effects of mycorrhizal root systems on performance of non-hosts in agricultural and natural ecosystems thus needs to be further evaluated.

The results of the present study can confirm earlier findings of the presence of arbuscular mycorrhizal fungi improving the performance of mycotrophic plants growing on saline soil. However, the relative contribution of the symbiosis to plant performance was not greater under salinity compared with non-saline conditions in the present study. When mycotrophic plants are grown on desert soils that did not harbor plants before, soil inoculation with arbuscular mycorrhiza fungal strains could be beneficial. Positive effects of mycorrhiza fungal root colonization appeared pretty robust in the present study, and were not affected in their magnitude by salinity or removal of shoot biomass. Risks of yield decline associated with the application of

biofertilizers based on mycorrhizal fungi to agricultural soils appear rather low. Arbuscular mycorrhiza fungal strains isolated from naturally saline ecosystems might have a greater potential to promote plant performance under salinity compared with the fungal population that was used in the present study.



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